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VERSLAGEN EN MEDEDELINGEN

DER

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VERENIGING
OVER HET JAAR 1955

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KONINKLIJKE NEDERLANDSE BOTANISCHE VERENIGING
AMSTERDAM

KONINKLIJKE
NEDERLANDSE BOTANISCHE VERENIGING
(Opgericht 15 Augustus 1845)

BESTUUR in 1955

Prof. Dr E. van Slogteren, voorzitter
Dr S.J. van Ooststroom, ondervoorzitter
Dr A. Quispel, 1e secretaris
Mej. Dr J. de Zeeuw, 2e secretaresse
Prof. Ir J.L. van Soest, penningmeester

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JAARVERSLAG VAN DE EERSTE SECRETARIS OVER 1955

Wanneer, zoals gebruikelijk, het jaarverslag begint met de herdenking van de leden, die wij dit jaar door de dood verloren, moet geconstateerd worden, dat deze verliezen dit jaar bijzonder zwaar waren. Onze twee ereleden: Prof. Dr A.A. Pulle en Dr P. Jansen overleden resp. op 28 februari en 2 april.

Prof. Dr A.A. Pulle, die de leeftijd van 77 jaar bereikte genoot grote bekendheid door zijn werk over de plantenwereld van Suriname, Zijn eerste kennis met de Surinaamse flora werd verkregen op een reis in 1902, welke reis later door verschillende andere gevolgd zou worden. In het jaar van zijn promotie, 1906, werd hij benoemd tot lector in de plantensystematiek en -geografie te Utrecht, waar hij in 1914 tot hoogleraar en directeur van het botanisch museum en herbarium werd benoemd. Talrijke systematische publikaties verschenen van zijn hand, veelal betrekking hebbend op de flora van Suriname, doch ook op die van Nieuw Guinea. Talrijk zijn ook de systematici, die zich zijn leerling mogen noemen. Hier willen wij hem echter in de eerste plaats herdenken wegens zijn enorme verdiensten voor onze vereniging. Deze kunnen wij niet beter beschrijven dan door de eenvoudige vermelding van het feit, dat hij sinds 1923 tot 1955 de zo zware taak vervulde van secretaris van de Commissie voor de redactie, eerst van het „Recueil", later van de „Acta". Ieder, die hem in deze functie heeft meegemaakt, weet hoeveel tijd en aandacht hij aan dit werk besteedde en hoezeer de uitgave van deze tijdschriften door hem gestimuleerd is. Daarnaast vervulde hij tijdelijk nog verschillende andere functies in de commissies van onze vereniging. Zijn verdiensten vonden erkenning in de benoeming tot erelid in 1945.

Dr P. Jansen werd 73 jaar oud. Ieder, die ook maar oppervlakkig met de floristiek heeft kennis gemaakt, zal de naam van P. Jansen zijn tegengekomen. Samen met Dr W. W. Wachter publiceerde hij immers talloze artikelen over de flora van Nederland en stelde hij een omvangrijk herbarium samen. Zijn grootste belangstelling ging hierbij steeds meer uit naar de grassen. Hoewel hij deze groep slechts als amateur bestudeerde (zijn vakwetenschap was immers de wiskunde) werd hij op dit gebied een zo allerwege erkend deskundige, dat hij in 1946 op grond van zijn botanische verdiensten het eredoctoraat van de Leidse universiteit ontving. In de laatste jaren van zijn leven breidde hij zijn studies ook uit tot de tropische grassen en bewerkte hij de Gramineen voor de „Flora Malesiana". Maar ook bij hem moet op deze plaats vooral gewezen worden op het vele werk, dat hij voor onze vereniging heeft verricht. Driemaal was hij penningmeester, hij was met slechts zeer korte onderbrekingen sinds 1924 lid van de Commissie tot redactie van het „Nederlandsch Kruidkundig Archief", sinds 1916 was hij secretaris en tenslotte voorzitter van de Commissie voor het floristisch onderzoek, en van 1927 af voorzitter van de subcommissie voor het Zuiderzee-onderzoek. In 1945 werd hij benoemd tot erelid als erkenning voor de voortreffelijke wijze, waarop hij in zovele functies onze vereniging heeft gediend.

Op 13 Januari overleed een onzer buitenlandse leden Prof. Dr G.H. Stahel. Hij was Zwitser van geboorte. In 1914 verzocht Prof.

Went hem een betrekking te aanvaarden op het landbouwproefstation te Paramaribo. Aanvankelijk was zijn werk daar beperkt tot fytopathologisch terrein, doch al spoedig wijdde hij zich aan de algehele wetenschappelijke exploratie van Suriname. In 1921 werd hij benoemd tot hoogleraar aan de landbouwhogeschool te Wageningen, doch spoedig begaf hij zich opnieuw naar zijn voornaamste studieterrein Suriname. Hij werd hier directeur van het proefstation, welke functie hij vervulde tot hij in 1948 gepensioneerd werd. In de necrologie, die prof. Pulle nog aan hem wijdde, werden de verdiensten van prof. Stahel aangeduid met de woorden: „De geniaalste en de veelzijdigste natuuronderzoeker, die Suriname ooit gekend heeft".

Tenslotte dient hier vermeld te worden, dat door het overlijden van Prof. Dr A.F. Blakeslee, waarvan het bericht ons dit jaar bereikte, de wereld niet slechts één der belangrijkste en veelzijdigste botanici, doch onze vereniging ook één zijner meest gewaardeerde corresponderende leden verloor.

Herdenken wij met grote eerbied de uitnemende botanici, wier grote verdiensten in het bovenstaande slechts kort konden worden aangestipt.

De samenstelling van het bestuur was in 1955 dezelfde als in 1954, De eerste secretaris, Dr A. Quispel, die moest aftreden, kon herkozen worden, daar hij bij een tussentijdse benoeming lid van het bestuur was geworden. Het aantal leden van de vereniging bleef vrijwel constant: het bedroeg eind december 1955 486, tegen 487 in december 1954. Hiervan zijn 62 leden student-lid. Het aantal corresponderende leden bedraagt 9.

Waar vorig jaar geconstateerd moest worden, dat de belangstelling voor de zomervergadering zoveel achterbleef bij de belangstelling voor de andere activiteiten kan dit jaar gelukkig vermeld worden, dat alle bijeenkomsten zich in een goede opkomst der leden mochten verheugen. Op zondag 30 januari werd te Utrecht de jaarvergadering gehouden. Op de wetenschappelijke vergadering 's middags sprak Dr H.J. Lam over zijn *„Reis naar Nieuw Guinea"*, terwijl de voorzitter Dr E. van Slogteren sprak over *„Een virusprobleem aan de Goudkust"* en daarbij een aldaar gemaakte film vertoonde. Zowel de voordrachten als de illustrerende film en kleurenfoto's werden door de aanwezigen zeer gewaardeerd.

De zomervergadering vond dit jaar plaats te Wageningen op 11 en 12 juni. De zaterdagmiddag was gereserveerd voor het bezoek aan een aantal Wageningse instituten nl. het Instituut voor bewaring en verwerking van tuinbouwproducten, het Instituut voor plantenziektekundig onderzoek, het Instituut voor de veredeling van tuinbouwgewassen en het Proefstation voor de zaadcontrole. Na de zeer geslaagde rondleidingen verzamelden de aanwezigen zich voor de gemeenschappelijke maaltijd in Hotel „de Wageningse Berg". Hier werd ook de avondvergadering gehouden, waar Mevr. Dr C.A. Reinders-Gouwentak sprak over *„De invloed van kunstlicht op de bloemaanleg van de tomaat"*. De volgende morgen ontving Prof. Dr H.J. Venema ons, waar hij na een inleiding over het werk op zijn instituut en in de botanische tuinen ons rondleidde door het Arboretum en het Arboretum Belmonte. Helaas werd de middagexcursie in wel zeer hevige mate door regen gestoord. Desondanks slaagden de excursieleiders Dr V. Westhoff, Dr D.M. de Vries en Ir F.M. Maas erin de aanwezigen een goede indruk te geven van de vegetatie langs de Grebbeberg, in een blauwgrasland en bij de bronnen nabij Oosterbeek.

De gebruikelijke zaterdagavondvergadering in october werd dit jaar vervangen door een „Symposium over het Soortsbegrip", dat zaterdag 8 october plaats vond. Teneinde alle leden in de gelegenheid te stellen deze bijeenkomst bij te wonen vond het symposium plaats in de middag en de vooravond. Voor de pauze sprak Dr C.G.G.J. van Steenis over „*Het soortsbegrip in de plantensystematiek*", terwijl na de pauze Dr M.J. Sirks „*Het soortsbegrip in de genetica*" en Dr J.E. Dinger „*Het soortsbegrip in de bacteriologie*" behandelden. De belangrijke voordrachten, de grote opkomst en de levendige discussies toonden, dat dit eerste symposium geslaagd genoemd mocht worden. Dit stimuleert het bestuur in de toekomst meerdere symposia te organiseren.

Ook de activiteiten van de Commissies en de belangstelling voor de hierdoor georganiseerde bijeenkomsten was over het algemeen zeer goed. Slechts moet hier even gewezen worden op het feit, dat gebleken is hoe sommige niet-leden zich herhaaldelijk op bepaalde commissievergaderingen laten introduceren zonder evenwel bereid te zijn lid van de vereniging te worden. Dit kan uiteraard niet de bedoeling van het introduceren zijn en het bestuur heeft daarom aan verschillende commissies het verzoek gericht hierop toe te zien en te bewerkstelligen, dat personen, die blijkens hun regelmatige aanwezigheid op bepaalde vergaderingen voldoende geinteresseerd zijn om lid te worden òf inderdaad als lid worden voorgesteld òf niet verder worden geintroduceerd. Ook ten aanzien van de contribuanten zal erop gelet moeten worden, dat geen personen contribuant worden, die door hun opleiding en/of werkzaamheid voor een volledig lidmaatschap in aanmerking komen.

Hoewel de finantiele toestand niet meer zo somber is als enkele jaren terug moet er terdege op gewezen worden, dat de finantien nog in een zeer labiele toestand verkeren. De uitgave van de kostbare „Acta" en „Flora" is alleen mogelijk door de subsidies, die wij ontvangen. Wij willen ook thans weer met grote dankbaarheid melding maken van deze belangrijke finantiele steun. Het Departement van onderwijs, kunsten en wetenschappen stelde ook dit jaar weer een subsidie van *f* 4000.- in het vooruitzicht. Het ligt in de bedoeling, dat dit bedrag komend jaar gecontinueerd zal worden door de „Organisatie voor zuiver wetenschappelijk onderzoek". De voorlopige toezegging hiervoor mochten wij reeds ontvangen. Met dankbaarheid maken wij ook melding van de gift van de „Hollandse maatschappij van wetenschappen" en van het „Hollands bloembollenhuis" te Lisse. Ook de overige donateurs en begunstigers zonden ons weer hun zozeer gewaardeerde bijdragen. Het zou wel zeer zijn toe te juichen indien het aantal donateurs kon worden uitgebreid. Het is immers niet à priori aan te nemen, dat wij uitsluitend onder de bloembollenkwekers de bereidheid tot subsidiering zouden aantreffen en wij willen hier nogmaals de hoop uitspreken, dat al die leden, die contact met de praktijk hebben, dit contact aanwenden om donateurs en eventueel begunstigers voor onze vereniging te winnen.

Na de genoemde bijdragen, die terwille van ons tijdschrift worden verleend, willen wij met dankbaarheid vermelden, hoe ook dit jaar weer de uitgave van de „Flora Neerlandica" gesteund werd, doordat de „Organisatie voor zuiver wetenschappelijk onderzoek" de salariering van de secretaris van de Flora voor haar rekening nam.

Wederom zag dit jaar een nieuw deel van de Acta het licht. De toevloed van de kopie vindt regelmatig voortgang. Bovendien werd op verzoek van het Committée ter huldiging van prof. Dr E. Reinders bij zijn afscheid als hoogleraar een extra nummer uitgegeven, waarin ook verschillende buitenlandse botanici een bijdrage plaatsten. Wederom kan met voldoening geconstateerd worden, dat voldoende kopie binnenkwam om vier goede gewone afleveringen van de Acta te doen verschijnen. Vermeld kan worden, dat de tot heden verschenen vier delen van de Acta door hun omvang en door de gevarieerdheid van de artikelen een representatief beeld geven van de activiteit der Nederlandse botanici. Toch zou een nog grotere toevloed van kopie mogelijk zijn en wij wekken dan ook nogmaals alle leden op hun wetenschappelijk werk in ons tijdschrift te publiceren.

Men bedenke, dat de Acta thans nog een der zeer weinige wetenschappelijke tijdschriften is, waar de artikelen onmiddellijk, dus zonder wachttijd, geplaatst kunnen worden. Verheugend is ook, dat dit jaar een stijging van het aantal betalende abonné's vertoonde, n.l. van 115 tot 138. Deze stijging is weliswaar klein, doch wij hopen, dat deze zich zal voortzetten. Op grond van dit, nog te gering, aantal abonné's werd de penningmeester toch reeds over 1955 een bedrag van *ƒ* 3248,71 door de uitgever toegezegd. De snelle buitenlandse reacties, die de meeste medewerkers op de in de Acta gepubliceerde artikelen ontvangen, wijzen er verder op, dat ons tijdschrift in het buitenland gezien wordt. Wij hopen, dat deze buitenlandse belangstelling zich niet zal beperken tot het aanvragen van overdrukjes, doch ook in een stijging van het aantal abonnementen zal worden waargenomen en wij wekken nogmaals ieder op bij zijn buitenlandse vakgenoten propaganda voor de Acta te maken. De uitgever liet hiertoe opnieuw een aantal exemplaren van de prospectus drukken en rondzenden.

Hoezeer de Acta dus reeds beantwoordt aan de bij de oprichting eraan gestelde eisen, er blijven bij sommige groepen in de vereniging nog wensen t.a.v. de publikatiemogelijkheid bestaan. Het plan bestond dit jaar een vergadering hierover te beleggen van bestuur, redactie en vertegenwoordigers van de commissies, die bij de publikatie belang hebben. Helaas moest deze vergadering tot tweemaal toe worden uitgesteld, eenmaal wegens het onverwacht overlijden van Dr Jansen, de tweede maal wegens een plotselinge Amerikaanse reis van de voorzitter. Wij hopen deze vergadering in het komend seizoen met beter succes te kunnen uitschrijven.

Hoewel het werk aan de Flora Neerlandica regelmatig voortgang vindt kon dit jaar nog geen nieuw deel worden afgesloten. De aanvragen uit het buitenland nemen steeds toe.

Zo kunnen wij met tevredenheid op het afgelopen jaar terugzien, een jaar, dat door grote activiteit gekenmerkt was. Toch mag deze tevredenheid ons niet de ogen doen sluiten voor de moeilijkheden, die nog steeds bestaan, voor de vaak te zeer tegenstrijdige wensen en belangen van de groepen in de vereniging en voor de afhankelijke finantiele toestand, die de activiteit mogelijk moet maken. Het overwinnen van deze moeilijkheden zal ongetwijfeld ook in het komende jaar tot de voornaamste zorg van het bestuur behoren.

Amsterdam 31 december 1955

De eerste secretaris
A. Quispel

VERSLAG VAN DE COMMISSIE VAN REDACTIE VOOR DE ACTA BOTANICA NEERLANDICA OVER 1955

Op 28 februari 1955 overleed Dr A.A. Pulle die vele jaren lang en tot zeer kort voor zijn dood secretaris van de redactie van het Recueil en van de Acta geweest was. Aan zijn nagedachtenis wijdde Dr J. Lanjouw een artikel in het eerste nummer van deel IV.

Het eerste nummer van Vol. IV verscheen op 12 mei 1955, het tweede nummer op 4 augustus. Er was dus enige vertraging in het verschijnen van deze afleveringen, voornamelijk tengevolge van het wat laat binnenkomen van de kopie. Met de drie daaropvolgende afleveringen (verschenen op 1 oktober, 21 oktober en 30 december) werd deze achterstand weer grotendeels ingehaald. De derde aflevering was dit jaar gewijd aan publikaties ter ere van Prof. Dr E. Reinders bij zijn aftreden als hoogleraar aan de Landbouwhogeschool te Wageningen.

Vol. IV werd afgesloten met 698 pagina's, bevattende 47 artikelen waar onder 3 dissertaties. In de loop van het jaar 1955 was dus de kopie-voorziening als geheel genomen zeer behoorlijk, tegen het eind van het jaar trad echter een schaarste van kopie in waardoor het verschijnen van het eerste nummer van de volgende jaargang zeker beinvloed zal worden.

Er werden in 1954 drie redactievergaderingen gehouden.

Aan het begin van het verslagjaar trad Dr A.A. Pulle af als lid en secretaris van de commissie, in zijn plaats werd Dr F.P. Jonker tot lid en secretaris benoemd.

Utrecht
januari 1956

De secretaris
F.P. Jonker

VERSLAG VAN DE COMMISSIE VOOR HET HERBARIUM, DE BIBLIOTHEEK EN HET ARCHIEF VAN DE KON. NED. BOTANISCHE VERENIGING OVER 1955

Het Herbarium werd verrijkt met 1732 Phanerogamen, geschonken door Ir T.W. Siertsema te Assen en omvattende het gedeelte van het herbarium van wijlen Prof. Dr L.H. Siertsema, dat nog niet in het verenigingsherbarium aanwezig was. Uitgeleend werden 302 exemplaren; het totaal aantal uitgeleende exemplaren bedroeg op 31 dec. van het verslagjaar 667 planten. Niet vermeld zijn hierbij de vele honderden nummers, die door leden van de staf van het Rijksherbarium voor hun werkzaamheden aan de Flora Neerlandica en door bezoekers werden onderzocht.

De in het vorige verslagjaar begonnen herrangschikking van het herbarium onder de moderne namen, werd door de amanuensis Hendriksen, onder leiding van de heer Reichgelt en ondergetekende beëindigd.

Uit de Bibliotheek zijn in het verslagjaar 1290 nummers uitgeleend. Aan boeken en overdrukken kwamen binnen 237 nummers, aan tijdschrift-afleveringen 512 exemplaren. Bij de overdrukken bevinden zich 47 nummers geschonken door de leden Andreas, Arisz, Heimans, van Ooststroom, van Soest, van Steenis en Vermeulen, 77 nummers geschonken door het Rijksherbarium, benevens het boek „Plantenammen yn Frysland", ontvangen van de leden Franke en van der Ploeg.

Leiden
23 januari 1956

De secretaris
S.J. van Ooststroom

VERSLAG VAN DE COMMISSIE VOOR HET FLORISTISCH ONDERZOEK VAN NEDERLAND OVER 1955

De Paas- en de Kerstvergadering werden beide gehouden te Amsterdam, op resp. 15 april en 28 december; beide vergaderingen werden wederom druk bezocht. Op de eerste vergadering werden de volgende voordrachten gehouden: E.W. Clason over „*Potamogeton-bastaarden*"; Dr S.J. van Ooststroom over „*Chenopodium crassifolium in Nederland*"; Ir J.L. van Soest over „*Taraxacum, sect. Vulgaria*"; H.H. Prell over „*Agropyron-soorten en over diverse plantenvondsten*"; ten slotte demonstreerde Mr J.H. van Wijk planten uit de Vendée. Op de tweede vergadering werd gesproken door Dr D. Bakker over „*Bastaarden van Scirpus, sectie Schoenoplectus*"; Th.J. Reichgelt over „*Diverse Nederlandse Cyperaceae*"; A. de Visser over „*Puccinellia in Zeeland*"; Dr S.J. van Ooststroom over „*Aanwinsten van de Nederlandse flora in 1954*"; Dr G. Kruseman over „*Een afwijkend ex. van Senecio vulgaris*"; Ir P. Tideman over „*Diverse Nederlandse Pteridophyta*"; J. van der Veer over „*Isoëtes-vondsten in N.-Brabant*"; E.W. Clason over „*De verspreiding van Ceratophyllum demersum en submersum in Nederland*"; Ir J.L. van Soest over „*Nieuwe Taraxacum-soorten uit Nederland*"; H.H. Prell over „*Agropyron-soorten*".

Enige dezer mededelingen zijn reeds in het tijdschrift gepubliceerd of zullen nog daarin verschijnen.

De zomerexcursie werd van 18 tot en met 22 juli gehouden in de omgeving van Sittard en stond onder leiding van Th.J. Reichgelt.

Leiden
23 januari 1956

De secretaris
S.J. van Ooststroom

VERSLAG VAN DE COMMISSIE VOOR DE BESCHERMING VAN DE WILDE FLORA OVER 1955

Tijdens de jaarvergadering van 1955 werd in de twee vacatures, ontstaan door het aftreden van Dr Ir W.H. Diemont en het bedanken als lid van Dr W.C. de Leeuw, voorzien door de benoeming van twee nieuwe commissieleden: Dr J. Wilcke en R.J. de Wit.

In het afgelopen jaar werd door de Directeur van het Staatsbosbeheer in een aantal gevallen het advies aan de commissie gevraagd over natuurbeschermingskwesties, waarbij bescherming van de flora op de voorgrond stond. Zo adviseerde de commissie over de bescherming van een groeiplaats van *Asplenium adiantum-nigrum* en *Asplenium trichomanes* in de gemeente Kamerik; over een voorstel tot overplanten van *Convolvulus lineatus* van de bedreigde groeiplaats in het Noordsloe naar een veiliger plaats; en over de bescherming van de groeiplaats van *Rubus saxatilis* in de bossen bij Ter Apel. Bovendien ontving de commissie van de Directeur van het Staatsbosbeheer ter beoordeling een lijst van in Nederland uitgestorven of zeldzame plantensoorten. Deze lijst werd door enkele leden van de commissie gecontroleerd en aangevuld.

De bescherming van het Wahlenbergiareservaat in de gemeente Tubbergen baart nog veel zorg. Ook hierover vond overleg plaats met het Staatsbosbeheer, terwijl verdere actie werd voorbereid.

Tenslotte werd door de commissie het initiatief genomen om te bereiken, dat in de toekomst beheersmaatregelen ten behoeve van de bescherming van groeiplaatsen van zeldzame planten zullen kunnen worden gesubsidieerd, ook wanneer het desbetreffende terrein eigendom is van een particulier.

Amsterdam
januari 1956

De wnd. Secretaris
R.J. de Wit

VERSLAG VAN DE COMMISSIE VOOR DE FYTOPATHOLOGIE OVER 1955

De Commissie voor de fytopathologie hield in 1955 twee vergaderingen. Op vrijdag 22 april 1955 werd een vergadering belegd in het botanisch laboratorium te Utrecht. Hier sprak Ir J. v. d. Ende over *„Enkele fysiologische problemen bij tuinbouwgewassen"* en Dr M.H. van Raalte over *„Groeistof of fungiciden als bescherming tegen plantenziekten"*. Op vrijdag 2 december spraken, eveneens te Utrecht, Ir H.A. van Hoof over *„Het mechanisme van de overbrenging van viren door luizen"* en G.J. Saaltink over *„Een verwelkingsziekte van lupine veroorzaakt door Fusarium oxysporum lupini"*.

In de vacature, ontstaan door het niet herkiesbaar aftreden van A.F.G. Slootweg werd voorzien door de benoeming van Ir D.H.M. van Slogteren tot lid van de commissie. In 1955 trad Dr K. Hartsuyker op als voorzitter en Dr D. Mulder als secretaris.

Wageningen
januari 1956

De secretaris
Dr D. Mulder

VERSLAG VAN DE COMMISSIE VOOR DE BIOSOCIOLOGIE EN HET VEENONDERZOEK VAN NEDERLAND OVER 1955

In de samenstelling van de commissie ontstond wijziging door het aftreden en niet herkiesbaar zijn van Dr F. Florschütz. In zijn plaats werd tot commissielid gekozen Dr H. Tj. Waterbolk.

Ook in dit verslagjaar organiseerde de commissie weer twee bijeenkomsten, de 35e en 36e Nederlandse dag voor biosociologie en palaeobotanie, resp. op 7 april en 22 december, de eerste in de collegezaal van het botanisch laboratorium van de Rijksuniversiteit te Utrecht, de laatste in het geologisch-mineralogisch instituut van deze Universiteit.

De 35e Dag werd bezocht door 24 leden en 6 introducé's. Achtereenvolgens spraken Ir Th. A. de Boer (Wageningen) over „*Resultaten en mogelijkheden van de graslandkartering*", met kleurenfoto's; Dr D. Bakker (Ens - N.O.P.) over „*Het disseminatie-spectrum van de vegetatie in de omgeving van het voormalige eiland Urk, II*" (mede namens Dr W. van der Zweep); Ir E. Stapelveld (Wijster) over „*De bodemvegetatie van Lariksbossen in Drente*"; Ir W.G. Beeftink (Goes) over „*De invloed van het zoutgehalte van het vloedwater op de vegetatie en molluskenfauna van de slikken en schorren langs Wester- en Oosterschelde*" en Ir L.G. Kop (De Lutte) over „*Vegetatie, bodem en groeikracht van de eik in enkele Twentse bossen*". Gedurende de middagpauze werd een gezamenlijke lunch gebruikt in het Universiteitshuis. Alle voordrachten werden gevolgd door een — soms levendige — discussie.

De 36e Dag werd bezocht door 73 personen, waaronder 27 introducé's. Het woord werd gevoerd door de volgende sprekers: Dr Ir W.H. Diemont (Maastricht) over „*Het wetenschappelijk verantwoord beheer van de Zuidlimburgse bosreservaten*"; Dr W. van Zeist (Groningen) over „*Enige absolute dateringen van een veenprofiel uit Zuidoost-Drente*"; A.W.H. Damman (Wageningen) over „*Een nieuwe indeling van de heidegezelschappen*"; Ir F. Maas (Wageningen) over „*Samenstelling en synoecologie van bronvegetaties*" en H. Doing Kraft (Wageningen) over „*De tegenwoordige opvattingen omtrent het associatiebegrip en de systematiek van plantengezelschappen*". Naar aanleiding van de inleiding van de Heer Doing Kraft, die tevoren een gestencilde samenvatting van zijn opvattingen beschikbaar had gesteld, werd uitvoerig gediscussieerd. Aan de discussie namen deel de Heren Barkman, Beeftink, Bekking, Maas, Meyer Drees, Westhoff en Zonneveld.

De tweede ondergetekende heeft bij de afwezigheid in het buitenland in december van Dr F.P. Jonker diens jaarverslag gecompleteerd met de gegevens betreffende de 36e Dag voor biosociologie en palaeobotanie, en tijdelijk het secretariaat op zich genomen.

Groningen
10 januari 1956

F.P. Jonker
H.T. Waterbolk

VERSLAG VAN DE COMMISSIE VOOR DE PLANTENFYSIOLOGIE OVER 1955

Op de jaarvergadering werd als opvolger van Mej. Dr C.J. Gorter, die niet herkiesbaar moest aftreden, benoemd Prof. Dr E.C. Wassink.

Er werden in het jaar 1955 twee vergaderingen gehouden. De eerste vergadering vond plaats op 4 juni 1955 in de collegezaal van het botanisch laboratorium te Utrecht. Tijdens de ochtendbijeenkomst sprak Dr R.J. Helder over: „*Opname en verdeling van gemerkt fosfaat bij* *jonge gerstplanten*, Dr W.K.H. Karstens, mede namens mevr. V. de Meester-Manger Cats en J.J. Gottenbos, over „*Groei en ontwikkeling van plantenweefsels in vitro met zetmeel als koolstofbron*" en J. Venekamp over „*Over de vorming en de betekenis van het asparagine in geëtioleerde kiemplanten van Lupinus luteus*". Na de lunch sprak eerst Ir J.A.D. Zeevaart (mede namens Dr Ir J.A. J. Stolwijk, over „*Bloei van Hyoscyamus niger in licht van verschillende spectraalgebieden*" en Dr B. Kok over „*Over een lichtremming in het fotosyntheseproces*". Om kwart over drie was het een bijzonder voorrecht Prof. E.I. Rabinowitch in ons midden te zien, die een voordracht hield over „*Fotosynthesis and related processes in bacteria, chloroplasts and chlorophyll solutions*". De vergadering werd bijgewoond door 50 leden. De middagvergadering werd georganiseerd in samenwerking met de fotobiologische kring.

De tweede vergadering vond plaats in de collegezaal van het laboratorium van N.V. Philips Gloeilampenfabrieken te Eindhoven op zaterdag 19 november. Voor deze vergadering hadden zich 60 leden opgegeven. Er werden vier voordrachten gehouden: D. Stegwee sprak over „*Enige aspecten van de purinestofwisseling bij Ophiostoma mutanten*", Dr J.S.C. Wessels over „*Nieuwste inzichten in de lichtreactie bij de fotosynthese*", Dr P. Massini over „*Tracer onderzoek in de fotosynthese*" en G. Meyer over „*De invloed van rood en blauw licht op planten*". Na afloop van deze voordrachten en de ons aangeboden broodmaaltijd volgde een rondleiding door de botanische afdeling van het laboratorium.

Amsterdam
31 december 1955

De secretaris
A. Quispel

VERSLAG VAN DE COMMISSIE VOOR DE PLANTENSYSTEMATIEK EN DE PLANTENGEOGRAFIE OVER 1955

In verband met het periodiek aftreden van Dr F.P. Jonker, die in 1954 voorzitter was en niet herkiesbaar, werd Dr J. Lanjouw als lid van de commissie aangewezen. Voorzitter in 1955 was Dr H.J. Venema.

De Commissie hield in het afgelopen jaar twee vergaderingen. De eerste bijeenkomst in Utrecht op 7 mei werd geleid door de wn. voorzitter Dr R. van der Wijk. Eerst sprak de Heer C. Kalkman over „*Een plantengeografische analyse van de Kleine Soendaeilanden*", daarna voerde A.C. van Bruggen het woord over „*Problemen bij de bewerking van het geslacht Payena D.C. (Sapotaceae)*". Dr F.P. Jonker sprak over „*De Marantaceae van Suriname*" en Mej. Dr A.M.W. Mennega over „*Enkele opmerkingen over het herkennen van Surinaamse bomen op de stam*". Tenslotte vertoonde Dr J. Lanjouw kleurenfoto's van Suriname en Arizona. De vergadering was bezocht door 20 leden en één introducé.

De tweede vergadering werd gehouden op 22 oktober te Amsterdam. Toen de voorzitter opende bleken 43 leden en 2 introducé's aanwezig. Dr P. van Royen, kort tevoren in ons land teruggekeerd, deed „*Enige mededelingen over de flora van Nieuw Guinea*", waarna P.A. Florschütz sprak over „*Het genus Octoblepharum (Musci)*" en Dr

L. van der Pijl over „*Vruchttypen en zaadverspreiding bij Leguminosae*". Daarna sprak Dr J. Heimans over „*Viola calaminaria en Viola alpestris*". Door gebrek aan tijd vervielen de beide andere voordrachten.

Amsterdam
31 december 1955

De secretaris
P. Vermeulen

VERSLAG VAN DE COMMISSIE TOT HET NAZIEN VAN REKENING EN VERANTWOORDING EN DE BESCHEIDEN VAN DE PENNINGMEESTER OVER 1955

Ondergetekenden, benoemd tot leden van de kascommissie op de j.l. gehouden jaarvergadering, verklaren hierbij, dat zij op 10 april ten huize van de penningmeester de boeken en bescheiden van de penningmeester hebben nagezien en gecontroleerd en die in orde hebben bevonden. Zij stellen aan het bestuur voor de penningmeester over het boekjaar 1955 décharge te verlenen.

Zij hebben er zich van overtuigd, dat het penningmeesterschap zeer veel tijd vergt en daar alle werkzaamheden in vrije tijd moeten geschieden, menen zij, dat de vereniging aan de penningmeester zeer veel dank verschuldigd is.

Hetwelk doende

Leiden/Amsterdam
11 april 1956

A.G. de Wilde
P. Vermeulen

VERLIES- EN WINSTREKENING OVER 1955

Kok Ankersmit fonds

Overdracht naar vrije fonds	1.100,-	Ontvangsten	1.735,61
Nadelig saldo koersverschil	293,18		
Saldo winst	342,43		
	1.735,61		1.735,61

Brumund fonds

Overdracht naar vrije fonds	700,-	Ontvangsten	950,13
Nadelig saldo koersverschil	320,03	Saldo verlies	69,90
	1.020,03		1.020,03

Vrije fonds

Lidmaatschappen	359,-	Contributies	8.141,90
Bibliotheek, herbarium, arch.	486,54	Ned. Kruidk. Arch.	131,50
Onkosten	976,13	Prodromus Flor. Bat.	10,50
Vergaderingen	196,22	Recueil. Trav. Bot. Neerl.	179,50
Jaarboek	615,61	Interest	557,96
Acta Botan. Neerl.	4.347,83	Overdracht Kok. Ank. fonds	1.100,-
Flora Neerl.	4.161,50	Overdracht Brumund-fonds	700,-
Nadelig saldo koersverschil	157,80	Voordelig saldo debit.	35,10
Saldo winst	249,68	Voordelig saldo credit.	693,85
	11.550,31		11.550,31

Acta Botanica Neerlandica

Acta deel IV uitg. 1955	17.817,54	Buitenlandse verkoop	2.549,26
credit.	4.364,-	Ontvangen aan overdrukken (incl. debit.)	2.847,-
Uitgaven voor dissertaties	1.638,67	Ontvangen aan dissert. (incl. debit.)	2.896,12
Balans a.p. bijdrage Rijk '54	4.000,-	Bijdrage Rijk '54	4.000,-
		Debit. Rijk '55	4.000,-
		Bijdrage laboratoria	3.150,-
		Bijdrage industrie	2.000,-
		Bijdrage Holl. Mij Wetensch.	500,-
		Bijdrage Kon. Ned. Bot. Ver.	4.347,83
		Diverse debiteuren	1.530,-
	27.820,21		27.820,21

BALANS, 31 DECEMBER 1955

Kok Ankersmit fonds

Effecten	36.971,08	Fonds per 1 I 55	39.761,56
Kas en Spaarbank	2.914,01	Saldo winst	342,43
Interest te innen	218,90		
	40.103,99		40.103,99

Brumund fonds

Effecten	19.469,45	Fonds per 1 I 55	27.170,61
Kas en Spaarbank	7.443,12		
Interest te innen	188,14		
Saldo verlies	69,90		
	27.170,61		27.170,61

Vrije fonds

Effecten	10.005,31	Fonds per 1 I 55	27.511,39
Kas en spaarbank	23.447,99	Contributies 1956	651,50
Debiteuren	6.248,66	Crediteuren	16.815,01
Contributie te innen	1.035,72	Saldo winst	249,68
Bijdrage Rijk 55 Acta (te innen)	4.000,-		
Interest te innen	489,90		
	45.227,58		45.227,58

BEGROTING 1956

Kok Ankersmit fonds

Inkomsten	1.330,-	Herbarium, bibliotheek, arch.	500,-
		Flora Neerlandica	700,-
		Natuurmonum. en Wahlenbergia	105,-
		Onkosten	25,-
	1.330,-		1.330,-

Brumund fonds

Inkomsten	800,-	Flora Neerlandica	650,-
		Commissies floristiek, Zuiderzee, wilde flora, systematiek, sociologie	100,-
		I. V. O. N.	25,-
		Onkosten	25,-
	800,-		800,-

Vrije fonds

Contributies	8.000,-	Vergaderingen	300,-
Interest	550,-	Onkosten	950,-
		Acta Botanica Neerl.	4.000,-
		Flora Neerl.	2.350,-
		Jaarboek	700,-
		Commissies fytopath. fysiol.	40,-
		Lidmaatschappen (zool. station; plantenziektekund. ver.; biol. raad; contactcomm. natuurbesch.; natuur en geneesk. congres; intern. natuurbesch.)	194,-
		Centr. Bureau Schimmel cult.	p; m.
		Onvoorzien	16,-
	8.550,-		8.550,-

Acta Botanica Neerlandica

Bijdrage vrije fonds	4.000,-	Uitgave 4 afleveringen	16.800,-
Bijdrage Z. W. O.	4.000,-	Onkosten redactie	100,-
Bijdrage industrie	2.000,-		
Bijdrage instituten	3.150,-		
Bijdrage Holl. Mij Wetensch.	500,-		
Verkoop 1955	3.240,-		
	16.900,-		16.900,-

Flora Neerlandica

Bijdrage Kok Ankersmit fonds	700,-	Uitgave	5.000,-
Bijdrage Brumund fonds	650,-	Onkosten redactie	200,-
Bijdrage vrije fonds	2.350,-		
Verkoop	1.500,-		
	5.200,-		5.200,-

NOTULEN VAN DE JAARVERGADERING, GEHOUDEN IN HET BOTANISCH LABORATORIUM TE UTRECHT OP ZONDAG 30 JANUARI 1955

Als de voorzitter Dr E. van Slogterom om 10.45 uur de vergadering opent zijn 29 leden aanwezig n.l.: Heimans, Heybroek, Houwink, Karstens, Kerling, Kern, Kleinhoonte, Koningsberger, Lanjouw, Jonker, Van Ooststroom, Prell, Quispel, Reichgelt, Roodenburg, D.H.M. van Slogteren, E. van Slogteren, Sobels, Van Soest, Van Steenis, Stegwee, Stomps, J.J. Swart, Vermeulen, De Visser Smits, R.J. de Wit, De Zeeuw, Zeylemaker en Zwillenberg en 1 introducé: Noerhadi.

De voorzitter herdenkt de leden, die in het afgelopen jaar zijn overleden: Arens, Reitsma, Ruys en Varossieau en doet mededeling van het overlijden van het lid Dr G. Stahel op 13 januari 1955, één van de oudste leden van de Vereniging.

Vervolgens worden de notulen van de in oktober te Amsterdam gehouden Ledenvergadering voorgelezen en goedgekeurd.

Daarna brengt de eerste secretaris zijn verslag uit over het jaar 1954. De ontwerp-jaarverslagen van de permanente commissies worden hierna voorgelezen en alle goedgekeurd. De voorzitter brengt aan alle secretarissen dank.

De penningmeester dient daarna zijn rekening en verantwoording in over 1954 en begint met een bespreking van de winst- en verliesrekening. Het saldo winst lijkt gunstiger voor het afgelopen jaar. Daarna volgt een bespreking van de verschillende fondsen en de begroting voor 1955. Nadat Dr Lanjouw om enkele informaties heeft gevraagd en Dr Koningsberger gesproken heeft over een subsidie door de Landbouworganisatie T.N.O. in verband met publikatie-mogelijkheid in de Acta, wordt de begroting aangenomen, waarna de voorzitter de penningmeester dankt voor zijn zorgvuldig beheer.

Tot leden van de Commissie tot nazien van de rekening en verantwoording en de bescheiden van de penningmeester over 1954 worden benoemd Mej. Dr Kleinhoonte en Dr Vermeulen, die beide de benoeming aanvaarden.

De candidaatleden per convocatie voorgesteld, worden alle bij acclamatie benoemd, evenals 2 leden, die met dispensatie van artikel 6, 1e lid der statuten staande de vergadering worden voorgesteld (Ir J.E. de Langhe en Mej. H.J. Pfältzer).

In de overige vacatures bij de Permanente Commissies worden, eveneens bij acclamatie, benoemd de leden, die per convocatie zijn voorgesteld.

Bij het bespreken van de vacature in de Commissie van Redactie voor de Acta botanica neerlandica, brengt de voorzitter de aftredende redactie-secretaris Dr A.A. Pulle veel dank voor al het werk, dat hij ook voor het nieuwe tijdschrift heeft gedaan. Deze dank zal aan Dr Pulle, die door ziekte niet aanwezig kan zijn, per brief worden overgebracht. Dr Jonker wordt tot redactie-secretaris benoemd.

Dr A. Quispel, die vorig jaar in verband met het aftreden van Dr van Herk tussentijds als eerste secretaris werd gekozen, wordt bij acclamatie herkozen.

Hierna volgen enkele mededelingen van de voorzitter over de Acta. De voorzitter haalt uit zijn 42-jarige lidmaatschap van de Botanische Vereniging enkele feiten op, en komt dan tot een bespreking van de laatste tijd. Hij wijst op het belang dat er voor de nu zo zeer gespecialiseerde botanici in ligt, om te proberen kennis te nemen, van wat er ook op andere botanische terreinen gepubliceerd wordt. De Acta, die nu gedurende enkele jaren zijn uitgegeven, zijn de enige band, die de verschillende groepen nog bijeenhoudt. Sinds enkele maanden worden er nu op niet altijd even gelukkige wijze wensen naar voren gebracht, die min of meer teruggaan naar de oude toestand, toen zowel Recueil als Krüidkundig Archief verschenen. Het bestuur is bereid dit nader te bespreken met voorzitters en secretarissen van de commissies en van de redactie-commissie.

Hierna wordt de vergadering geschorst voor de gemeenschappelijke lunch in het Universiteitshuis.

Om 14 uur wordt de vergadering heropend door de voorzitter. Thans zijn nog 10 leden aanwezig, die de ochtendvergadering niet bezochten n.l.: Von Arx, Von Arx-van der Brugge, Bakhuizen Van den Brink, Casparé, Docters van Leeuwen, P. van Eck, P.A. Florschütz, J. Th. Koster, Leeuwenberg en Lens.

Dr Lam spreekt over zijn „*Reis naar Nieuw-Guinea*", en geeft ons aan de hand van fraaie kleurenfoto's een indruk van het gebied dat hij bezocht. Hij was ook in het Australische gedeelte van Nieuw-Guinea en vloog van daar naar Hollandia. Hij toonde ons beelden van de droge Zuidkant en van de veel vochtiger Noordkant, van een regenwoud aan de baai bij Hollandia, terwijl ook enkele foto's ons de bijzonder mooie versiering van de prauwen met vogels- en visfiguren lieten zien.

Ook van zijn tocht door West- en Z-Australië gaf Dr Lam ons interessante beelden van de plantengroei, terwijl hij tevens zijn bezoek aan Baas Becking in Sydney vermeldde.

Na een korte theepauze fungeert Dr Van Ooststroom als voorzitter en geeft het woord aan Dr Van Slogteren die spreekt over „*Een virusprobleem aan de Goudkust*".

De ziekte in de cacao, die aanvankelijk niet herkend werd, was reeds in 1925 begonnen en aan de hand van kleuren- en zwart-wit dia's liet de spreker ons zien, welke een groot gebied in 1948 reeds sterk of minder sterk was aangetast. De ziekte bleek een virusziekte te zijn, en alleen te bestrijden door omhakken van de cacao-aanplant, aangezien sproeien door gebrek aan water onmogelijk was. Behalve Dr Van Slogteren waren ook Dr Carter van Hawaii en Dr Berkeley uit Canada naar de Goudkust gekomen om dit probleem van de technische en ook van de paedagogische kant te bekijken. Enkele fraaie opnamen gaven ons een beeld van de bijeenkomsten, die met de bevolking gehouden werden. Nadat de spreker enkele vragen beantwoord had, werd de vergadering, nadat nog melding was gemaakt van het overlijden van Prof. Falck en Prof. Tischler, gesloten.

11 juni 1955

De voorzitter
E. van Slogteren

De 2e secretaresse:
J. de Zeeuw

NOTULEN VAN DE ZOMERVERGADERING MET EXCURSIES OP ZATERDAG 11 EN ZONDAG 12 JUNI 1955 TE WAGENINGEN

De Zomervergadering had op zaterdagavond 11 juni plaats in de zaal van Hotel „De Wageningse Berg" te Wageningen. 's Middags was hieraan voorafgegaan een bezoek aan verschillende Wageningse Instituten n.l. aan het Instituut voor bewaring en verwerking van tuinbouwproducten, Instituut voor veredeling van tuinbouwgewassen, Instituut voor plantenziektekundig onderzoek, en het Rijksproefstation voor zaadcontrole. De bezoekers waren over het algemeen enthousiast over hetgeen hun op de verschillende Instituten getoond werd.

Om 18.15 uur volgde een gemeenschappelijke maaltijd in Hotel „De Wageningse Berg", gedurende welke de stemming, mede dank zij de aanwezigheid van Prof. Gregory uit Londen zo geanimeerd was, dat pas om half 9 de Algemene Vergadering geopend kon worden.

Aanwezig waren de leden: Anker, Bremer-Reinders, De Bruin-Brink, De Bruyn, Casparé, Maas Geesteranus, A. Gorter, Chr.J. Gorter, Harmsen, Hartsema, Hegnauer, Kamerbeek, Karstens, Kreulen, Löhnis, Oortwijn Botjes, Van Ooststroom, Polak, Quispel, Radersma, Reinders, Reinders-Gouwentak, E. van Slogteren, Slooff, Spierenburg, Thung, Wassink, De Zeeuw, Zeijlemaker en 4 introducé's.

De notulen van de jaarvergadering gehouden op 30 januari 1955 te Utrecht worden voorgelezen en goedgekeurd. Hierna verzoekt de voorzitter enkele ogenblikken stilte voor de beide ereleden Dr Pulle en Dr Jansen, die ons in de afgelopen maanden door de dood ontnomen zijn.

De beide op de convocatie voorgestelde leden Jensma en Mej. Wertheim worden benoemd.

De 1e secretaris deelt mede, dat de Commissie tot het nazien van de rekening en verantwoording over 1954 van de penningmeester de betreffende stukken in orde heeft bevonden, waarop de penningmeester gedechargeerd wordt.

Daarna volgt het wetenschappelijke gedeelte, waarin Mevr. Dr C.A. Reinders-Gouwentak spreekt over *„De invloed van kunstlicht op de bloemaanleg van de tomaat"*.

Bij gebruik van kunstlicht kan de cultuur van tomaten in de winter later aanvangen. Dit spaart brandstof, arbeidsloon enz. Vergelijking met de teelt op Guernsey toont, dat de factoren licht en temperatuur daar veel gunstiger zijn.

De historische ontwikkeling van het gebruik van kunstlicht, uitsluitend of tezamen met daglicht werd besproken.

Dia's welke het dn karakter van de tomaat tonen en lantaarnplaatjes van ld.- en kd.-planten werden besproken. Het blijkt, dat de dn tomaat ook een daglengte effect bezit, hetwelk verschillend is al naar de duur en de aard van de belichting.

De aanleg van een bepaald aantal bladeren schijnt van meer betekenis te zijn voor de bloemaanleg dan de aanwezigheid van dat bepaalde aantal. Kort is ingegaan op de mogelijke betekenis van het proces van blad-aanleg voor het bloeirijp worden.

Nadat de spreekster enkele vragen heeft beantwoord, sluit de Voorzitter om 10.15 uur de vergadering.

Op zondag 12 juni verzamelen de deelnemers zich om 9.45 uur in de collegezaal van het Laboratorium voor plantensystematiek en -geografie, waar Dr Venema een inleiding houdt over: „*De organisatie en het werk van de botanische tuinen en het Belmonte Arboretum te Wageningen*".

Spreker vertelt o.m. een en ander over het werk, dat in nauw overleg met de kwekers wordt uitgevoerd zowel in het oude Arboretum, als in het Belmonte Arboretum, als ook in de tuin aan het Spijk. De bedoeling hiervan is, om zowel voor bloemheesters als vaste planten te geraken tot een sortimentsbeperking, waarbij alleen die tuinvariëteiten die bijzondere waarde hebben voor de tuinen, zullen worden aangehouden. Tevens worden de benamingen van de siergewassen gecontroleerd, en hun herkomst opgespoord. Goede beschrijvingen zijn zeer zeldzaam, vandaar dat veel aandacht geschonken wordt aan een juiste karakterisering van de verschillende vormen. Beschrijvingen alleen zijn echter niet voldoende. De beschrijvingen worden dan ook aangevuld met detailtekeningen, aquarellen, foto's, enz. Onder het nuttigen van een kopje koffie werd een fraaie collectie tekeningen en aquarellen van bloemen en vruchten der in cultuur zijnde vaste Papavers bekeken. Hierna werd een rondwandeling door het Arboretum gemaakt, waarbij we de Papavers ook op het veld te zien kregen. Na een kort bezoek aan het in aanleg zijnde Belmonte Arboretum vertrokken de deelnemers naar de Grebbesluis, waar de lunch gebruikt werd in Hotel de Grebbe. Aanwezig waren toen 31 leden, n.l.: Blaauw-Jansen, De Bruin-Brink, De Bruyn, Casparé, J.Z. van Dijk, Chr.J.Gorter, Harmsen, Hartsema, Hegnauer, Hekking, Jensma, Kamerbeek, Karstens, Kreulen, Löhnis, Oortwijn Botjes, Polak, Quispel, Reinders, Reinders-Gouwentak, Reijnders, E. van Slogteren, Slooff, J.J. Swart, Terpstra, Tideman, D.M. de Vries, Wassink, Westhoff, De Zeeuw, Zeijlemaker + 3 introducé's, van wie Dr Westhoff, Dr D.M. de Vries en Ir J.F. Maas de leiding van de middagexcursie op zich zouden nemen.

Om 14 uur werd begonnen met een korte wandeling langs de voet van de Grebbeberg, waarna de bus ons bracht naar het Blauwgraslandreservaat in Bennekom en de bronnen op de Hemelse Berg te Oosterbeek. Om 17.30 uur waren de meeste deelnemers aan het station Arnhem, vanwaar zij weer naar hun woonplaatsen vertrokken.

8 oktober 1955

De voorzitter
E. van Slogteren

Dr 2e secretaresse
J. de Zeeuw

NOTULEN VAN DE ALGEMENE LEDENVERGADERING GEHOUDEN TE AMSTERDAM OP ZATERDAG 8 OKTOBER 1955

Als de Voorzitter om 15.30 uur de vergadering opent, blijkt uit de grote opkomst de belangstelling der leden, terwijl ook een groot aantal introducé's, voornamelijk leden van de VeLebi, aanwezig is, n.l. 70 leden: Anker, Van Asperen de Boer, Bakhuizen van den Brink, Bakker, Becker, Beeftink, Belderok, Beumé, Van Beverwijk, A.J. Bianchi, F. Bianchi, Boshuizen, Bosschaert, De Bruyn, Bruinsma, Casparé, J. Dijkstra, F.H. Feekes, Frahm-Leliveld, H.P. Maas Geesteranus, A. Gorter, Groenhuijzen, E.E. Harmsen, Heimans, Hendriks, Van Herk, Houwink, Huisinga, Janse, Jensma, Jonker, Karstens, Kerling, Kern, Lam, Lanjouw, Lens, Mechelink, A. Mennega, Meijers, Meyknecht, Muller, Van Nigteveld, Van de Houven van Oordt-Hulshof, Oosterhuis, Van Ooststroom, Quispel, Radersma, Reichgelt, Reijnders, Salverda, Segal, Sirks, E. van Slogteren, Slooff, De Visser Smits, Sonneveld, Stafleu, Van Steenis, Stomps, J.J. Swart, Vermeulen, Vreede, Vroman, Van der Wijk, Wildervanck, H.C.D. de Wit, De Zeeuw, Zeijlemaker en 27 introducé's.

De notulen van de zomervergadering gehouden te Wageningen op zaterdag 11 en zondag 12 juni 1955 worden voorgelezen en goedgekeurd.

De beide candidaat-leden per convocatie voorgesteld worden bij acclamatie benoemd, evenals twee leden, die met dispensatie van artikel 6, 1e lid der statuten, staande de vergadering worden voorgesteld (E.E. van der Voo en O.L. Staden).

Nadat Dr S.E. de Jongh benoemd is als lid van de Commissie voor het floristisch onderzoek van Nederland wordt overgegaan tot het wetenschappelijk gedeelte, dat uit een „*Symposium over het soortsbegrip*" bestaat.

Als eerste spreker krijgt Dr Van Steenis het woord voor zijn voordracht: „*Het soortsbegrip in de plantensystematiek*". Hij onderstreepte de ontzaglijke verantwoordelijkheid van de systematicus, die de enige volledige autonome grondslag moet leveren voor zuivere en toegepaste botanie, aangezien geen enkel botanisch onderzoek kan werken met anonieme planten. De mogelijkheid van classificatie en dus van naamgeving berust op het overal aanwezig zijn van discontinuiteiten, grote en kleine. Het komt er op aan voor de soortsomgrenzing uit de velerlei discontinuiteiten zodanige te kiezen, dat de verkregen onderscheiding ook voor anderen praktisch bruikbaar is: de klassieke werkwijze. Dieper gaande achtte Spreker, na toetsing van vele opvattingen, Danser's voorstel de grenzen van diens *commiscuum* te doen samenvallen met de soortsgrenzen, vermoedelijk de beste benadering. Hiermee zouden vele genitici instemmen. Apomicten bieden andere mogelijkheden.

Na afloop van deze voordracht bestond er gelegenheid in korte tijd een door de staf van het laboratorium keurig verzorgde broodmaaltijd te nuttigen.

Dr Sirks spreekt daarna over: „*Het soortsbegrip in de genetica*". De cytogenetica kan hulp bieden aan de genetica, hoewel men tegenover het chromosomenportret als soortskenmerk met de nodige reserve moet staan, aangezien de variabiliteit binnen de soort niet bekend is. De spreker behandelt aan de hand van een aantal diapositieven enige voorbeelden van de problemen, die men in dit gebied ontmoet.

Als laatste sprak Dr Dinger over: *„Het soortsbegrip in de bacteriologie"*.

Bij de omgrenzing van de soort in de bacteriologie is de keuze wat wel en wat niet in één soort samen te brengen is afhankelijk van de opvatting van de wetenschappelijke onderzoeker.

Besproken wordt het systeem van Bergey, 't welk in de medische bacteriologie thans internationaal in gebruik is.

Een bijzondere moeilijkheid om in de bacteriologie de criteria voor soortomgrenzing vast te stellen ligt in de grote veranderlijkheid der bacteriën. De oorzakelijke factoren, welke deze veranderlijkheid teweegbrengen vormen reeds lang een onderwerp van studie, de veranderingen kunnen zijn van faenotypische en genotypische aard. Bij de verandering van het genotype komt de mogelijkheid van overdracht van erfelijke eigenschappen ter sprake, waarbij blijkt dat genetisch materiaal op drie wijzen kan worden uitgewisseld in de wereld der micro-organismen.

Voor de begrips-omgrenzing van de soort komen deze laatste verschijnselen voorshands uit praktische overwegingen niet in aanmerking.

Na afloop van deze voordracht wordt enige tijd aan de discussie besteed, waarbij eerst de lezing van Dr Sirks aan de orde komt, daarna die van Dr Van Steenis en tenslotte de door Dr Dinger gehouden voordracht.

Nadat Dr Stomps nog de mogelijkheid van het op schrift stellen van deze voordrachten ter verspreiding onder belangstellenden ter sprake heeft gebracht, sluit de voorzitter om ± 20.15 uur de vergadering.

De voorzitter	De 2e secretaresse
Dr E. van Slogteren	Dr J. de Zeeuw

KORTE SAMENVATTINGEN VAN ENKELE VOORDRACHTEN GEHOUDEN IN DE COMMISSIEVERGADERINGEN

COMMISSIE VOOR DE FYTOPATHOLOGIE

Ir J. van den Ende: Enkele fysiologische problemen bij tuinbouwgewassen.

Wanneer de verdamping de wateropname tijdelijk te veel overtreft kunnen bij tal van gewassen fysiologische ziekten optreden, zoals rand bij sla, waterziek bij bloemkool, neusrot en waterziek bij tomaten en lamsteligheid bij druiven. Door de bijzondere klimatologische omstandigheden komen dergelijke ziekten vooral voor bij de teelten onder glas.

De maatregelen ter voorkoming van deze ziekten moeten enerzijds gericht zijn op een goede watervoorziening en op een beperking van de verdamping tijdens kritieke weersomstandigheden en anderzijds op het verkrijgen van een weinig gevoelig gewas. Door allerlei cultuurmaatregelen kan het kasklimaat worden beïnvloed. Door het juist uitvoeren van dergelijke maatregelen kan men de voor de fysiogene ziekten kritieke omstandigheden beperken en kan men het gewas aanvankelijk afharden. De regeling van de omstandigheden in de grond komen vooral neer op een goede watervoorziening en op het handhaven van een goede osmotische waarde van het bodemvocht. Deze waarde zal enerzijds niet te hoog en anderzijds niet te laag mogen zijn.

Naast het waterleverend vermogen van de bodem en de wateronttrekkende kracht van de atmosfeer zijn de inwendige factoren, die de wateropname en waterafgifte beïnvloeden, van belang voor het optreden van de fysiogene ziekten. Voorts zijn tal van verschijnselen hierbij slechts te verklaren door interne waterverplaatsingen. Bij een nadere bestudering van de omstandigheden, waaronder de afwijkingen zich voordoen, zal men dus ook de waterhuishouding van de plant dienen te onderzoeken. Enkele bruikbare onderzoekmethoden zijn: het verrichten van groeimetingen, het meten van de zuigkracht van weefsels en van de osmotische waarde van het celsap en het vaststellen van de openingstoestand van de huidmondjes.

Het organisch-chemische onderzoek van de plant zal van belang kunnen zijn voor het inzicht in de aard van de verschijnselen.

Literatuur:

J. van den Ende: Groeiafwijkingen die samenhangen met de waterhuishouding in de plant. Mededelingen Directeur van de Tuinbouw 17, 1954: 615-636. J. v. d. Ende: Welke eisen stellen tomaten aan de watervoorziening? (zal verschijnen in november Mededelingen Directeur van de Tuinbouw 1955).

Dr M.H. van Raalte: Groeistof of fungiciden als bescherming tegen plantenziekten.

In een onderzoek van Dimond en zijn medewerkers werd gevonden, dat de symptomen van de aantasting van tomaten door *Fusarium oxysporum lycopersici* minder ernstig waren bij planten, die met groeistoffen waren behandeld, dan bij onbehandelde planten. Hieruit leidden zij af, dat de groeistoffen door inwerking op de stofwisseling de resistentie van de planten verhoogden. Sindsdien werd door deze onderzoekers ook in vele andere gevallen aangenomen, dat ook verbindingen, die geen duidelijke groeistofwerking hadden, doch wel in de plant een bescherming tegen ziekte teweegbrachten, dit laatste via de stofwisseling van de plant deden. Deze hypothese heeft de zwakke grondslag; als één verbinding in één geval therapeutisch werkt via de stofwisseling, doen alle verbindingen het langs die weg.

Spreker en zijn medewerkers werden met dit probleem geconfronteerd, toen bleek, dat S-carboxymethyl.-N.N.-diamethyl dithiocarbaminaat, een verbinding, die komkommers enigszins tegen het vruchtvuur beschermt, groeistofeigenschappen bezat. Door substitutie van de twee waterstofatomen aan het koolstofatoom dat aan de carboxylgroep grenst, werd een verbinding verkregen, die geen groeistofeigenschappen had, doch wel komkommerplantjes tegen de ziekte beschermde. Het samengaan van de groeistofwerking met de beschermende werking was dus geen vereiste voor de eerste. Mogelijk is echter, dat een groeistofachtige structuur verbindingen gemakkelijk verplaatsbaar maakt, en dat daardoor in de langzaam groeiende apotheek van de inwendige therapie groeistoffen nogal eens voorkomen.

Ir H.A. van Hoof: Het mechanisme van de overbrenging van viren door luizen.

Ir van Hoof probeerde een dieper inzicht te verschaffen in het mechanisme waarop de virusoverbrenging bij bladluizen berust. Allereerst besprak hij in grote trekken de manier waarop de plantenviren in de natuur worden verspreid. Vooral de wijze waarop planten door grondviren worden aangetast is nog een vraagstuk. Het tabaksmozaiek-virus is zeer nauwkeurig bestudeerd. Door verschillende auteurs werd een verklaring gezocht van het feit, dat bladluizen dit virus niet kunnen overbrengen. De verschillende theorieën die hieromtrent werden opgesteld, werden in het kort besproken. De persistente en nonpersistente viren en de theorieën en feiten die over het mechanisme van de overbrenging door de luis hierbij door verschillende onderzoekers naar voren werden gebracht, vormden een belangrijk onderdeel van deze voordracht.

Hierna besprak Ir van Hoof enkele van zijn eigen proeven: Als proefobject dienden de luis *Myzus persicae*, het Lupine-mozaiek virus en de Tuinboon.

Met behulp van plastic en nylongaas werd een plantencel nagebootst, waarin een druk van 7-12 atm. werd aangebracht. Voorts werd de wijze waarop de luis zijn stiletten in de plant brengt en de vorming van het speekselkanaal bestudeerd. De spreker toonde enige fraaie electronen microscopische foto's van de stiletten van de luis.

Aan de hand van deze proeven bracht hij een eigen theorie over de overbrenging naar voren die echter, daar zijn onderzoek nog niet beeindigd is, als een voorlopige moet worden beschouwd.

G.J. Saaltink: Een verwelkingsziekte van Lupine veroorzaakt door *Fusarium oxysporum lupini*.

Bij de teelt van *Lupine luteus L.* blijkt een verwelkingsziekte van veel belang te zijn. Het verwelken van de bladeren is een belangrijk ziektesymptoom.

Een aangetaste plant sterft enkele maanden te vroeg af. De ziekte wordt veroorzaakt door de schimmel *Fusarium oxysporum* Sn. en H., die de planten binnendringt vanuit de bodem. Het mycelium groeit daarna voornamelijk in de xyleemvaten. Op een besmet veld vertonen vatbare planten in juni symptomen, terwijl planten van resistente selecties geen symptomen te zien geven.

Volgens drie methoden is de aanwezigheid van de schimmel in lupine planten vastgesteld. 1. Uitleggen van delen van de planten op een voedingsmedium. 2. Anatomisch onderzoek. 3. Het fijnmalen van delen van planten in een mixer (waring-blendor). Enkele c. cm. van de verkregen suspensie worden met agar gemengd en gegoten. Het opkomen van *Fusarium* kolonies wijst op de aanwezigheid van de schimmel. Bovendien is het aantal kolonies een maat voor de hoeveelheid schimmel in de plant. In resistente planten kan de schimmel met deze methode eveneens worden aangetoond. De uitbreiding van de schimmel is in deze planten echter minder sterk dan in vatbare planten. Thans wordt gezocht naar een verklaring voor de verschillende uitbreidingsmogelijkheid van de parasiet in resistente en vatbare planten.

COMMISSIE VOOR DE BIOSOCIOLOGIE

E. Stapelveld: De bodemvegetatie van Larix bossen in Drente.

In aansluiting op een vergelijkend onderzoek van het bosbouwproefstation T.N.O. te Wageningen (naar het verband tussen bodem en opstandsgroei), werd in dezelfde objecten de vegetatie bestudeerd. Daarbij konden voorlopig drie vegetatie-typen worden onderscheiden. Het *Corydalis-Larix-type* met als differentiërende soorten: *Corydalis claviculata, Holcus mollis, Urtica dioica, Rubus idaeus, Galeopsis tetrahit, Ranunculus repens* e.a. Het *Dicranum-Larix-type*, met als diff. soorten: *Dicranum undulatum, Polytrichum juniperinum, Calluna vulgaris, Lophocolea bidentata* e.a., en het *Festuca-Larix*-type, dat geen eigen diff. soorten heeft, maar wel een aantal gezamenlijk met het D.L.-type: *Molinia coerulea, Festuca ovina, Plagiothecium undulatum, Anthoxanthum odoratum, Ptilium crista-castrensis* en *Campylopus flexuosus*. Er bleek een nauw verband te bestaan tussen deze vegetatie-typen en het fosfaatgehalte van de bodem, in die zin dat het C.L.-type aan fosfaatrijke grond gebonden is, en het D.L.-type aan fosfaatarme grond. Het F.L.-type staat daar tussenin. Binnen elk vegetatie-type zijn nog enkele floristische verschillen waar te nemen, die corresponderen met het stikstofgehalte, de pH of de waterhuishouding van de bodem. Zij zijn echter niet duidelijk genoeg, om daarop een verdere indeling in sub-typen te baseren. Waarschijnlijk hebben de vegetaties in de (nog jonge) lariksbossen van Drente hun evenwichtstoestand nog niet bereikt. De vegetatie-typen blijken goede indicatoren te zijn voor de groei van de lariks, en leveren dus een goed bruikbare basis voor vegetatiekartering ten dienste van de bosbouw.

Ir W.G. Beeftink: De invloed van het zoutgehalte van het vloedwater op de vegetatie en Molluskenfauna langs de Wester- en Ooster-Schelde.

In de Westerschelde neemt het zoutgehalte van het vloedwater eerst langzaam, daarna sneller af. De schommeling om het gemiddelde neemt echter van West naar Oost toe, hetgeen wordt veroorzaakt door de zoetwaterafvoer van de rivier de Schelde. Het zoutgehalte in de Oosterschelde is gemiddeld 27.75 o/oo NaCl, de variatie wordt teweeggebracht door de zoetwaterafvoer van de Lek, Waal en Maas.

De vegetatie en molluskenfauna is onderzocht op 7 schorren, gelegen langs de Noordelijke oever van de Westerschelde vanaf de Kaloot tot de Belgische grens, en in het Oosterschelde-bekken op enkele schorren in de Zandkreek en de Eendracht. Op de slikken en schorren van het Oosterschelde-bekken komen de volgende gezelschappen voor: *Zostera nana-sociatie*, *Salicornietum europaeae*, *Spartinetum strictae*, *Puccinellietum maritimae*, *Obione portulacoides-sociatie*, *Artemisietum maritimae*, *Agropyron litorale-sociatie*, *Armerieto-Festucetum*. Langs de Westerschelde zijn de drie eerste geheel door *Spartina townsendii* verdrongen.

De samenstelling van de plantengezelschappen langs het Oosterschelde-bekken verandert van West naar Oost niet, langs de Westerschelde wel. De *Obione portulacoides-sociatie* is bij Waarde verdwenen. De rijkdom van de vegetaties neemt af, vnl. omdat *Salicornia europaea*, *Suaeda maritima*, *Artemisia maritima*, *Obione portulacoïdes* en *Limonium vulgare* verdwijnen. Het schor is het soortenarmst, als de schommeling in het zoutgehalte van het vloedwater maximaal is (Ossendrecht). Van de Mollusken komen *Hydrobia ulvae* en *Phytia myosotis* langs de Westerschelde alleen ten Westen van Bath voor, *Assiminea grayana* neemt van West naar Oost steeds meer in massa en oecologische amplitude toe.

Ir L.G. Kop: Vegetatie, bodem en groeikracht van de eik in enkele Twentse bossen.

In Twente en de Achterhoek werd van enkele bossen de vegetatie vergeleken met enige gemeten bodemfactoren en met de groeikracht van de eik.

Onderscheiden werden: 1. het eikenberkenbos, 2. het droge, arme eikenhaagbeukenbos, 3. het vochtige, rijke eikenhaagbeukenbos, 4. het beekbos.

Het tweede type staat in floristische samenstelling tussen eikenberkenbos en eikenhaagbeukenbos in. De struiklaag bevat hazelaar en zoete kers naast lijsterbes en vuilboom. In de kruidlaag vindt men soorten uit het *Quercion* naast soorten uit de *Querceto-Fagetea* zoals *Hedera Helix*, *Stellaria holostea* en soms ook *Lamium Galeobdolon* en *Anemone nemorosa*.

Het derde type bevat slechts weinig *Quercion*-soorten en een grote groep, die zowel grote vochtigheid als grote basenrijkdom kan indiceren. De belangrijkste daarvan zijn: *Geum urbanum*, *Fraxinus excelsior*, *Adoxa moschatellina* en *Primula elatior*. In de struiklaag voeren es en hazelaar de boventoon, terwijl de es ook een belangrijke plaats in de boométage inneemt.

In het beekbos treft men de zelfde groep soorten aan, maar dan nog uitgebreid met bijv. *Prunus Padus*, *Urtica dioica*, *Aegopodium Podagraria* en *Rumex sanguineus*. *Carpinus Betulus*, *Prunus avium* en *Stellaria holostea* daarentegen – de kensoorten van het *Querceto-Carpinetum* em. *Oberdorfer* – komen veel minder voor dan in de vorige twee typen.

De bodemanalysen gaven een vrij laag resultaat. De bodem van het tweede type bleek in de bovengrond een zône te omvatten, die zeer arm aan basen is, terwijl het derde type een bodem had, die over het gehele profiel basenrijk bleek te zijn. In twee gevallen, dat het eerste met het tweede type kon worden vergeleken, kon echter niet geconcludeerd worden tot een belangrijk bodemverschil. Vermoedelijk zijn de beslissende factoren niet gemeten.

De boniteit van de eik daarentegen gaf een duidelijke correlatie met de vegetatietypen. De groei is het best in het derde type, het slechtst in het eerste, terwijl het vierde een uiteenlopend beeld te zien gaf.

Dr Ir W.H. Diemont: Over het wetenschappelijk verantwoorde beheer van de Zuid-Limburgse bosreservaten.

Gedurende de laatste jaren heeft het Ministerie van Onderwijs, Kunsten en Wetenschappen langs de Maas en de Geul in Zuidlimburg belangrijke oppervlakten hellingbos aangekocht met op de eerste plaats de bedoeling, om in deze reservaten aan de steeds meer bedreigde wilde flora en fauna toevluchtsoorden te verschaffen en om geologische, archaeologische en bodemkundige merkwaardigheden veilig te stellen. Het beheer dezer bossen zal dus dienovereenkomstig moeten worden gevoerd.

De oorspronkelijke bosflora heeft in het verleden plaatselijk wijzigingen ondergaan door ondeskundige uitkap, door eeuwenlange slaghoutexploitatie en door het inplanten van exotische houtsoorten. Dergelijke bosgedeelten zullen hervormd dienen te worden met boom- en struiksoorten uit het van nature aanwezige bos.

Ter voorkoming van beschadigingen van de te beschermen flora en fauna, zullen voor het begin van de bosbouwkundige werkzaamheden plannen tot instandhouding en van verbetering van de reservaten moeten worden opgesteld. Dergelijke plannen kunnen worden gebaseerd op fytosociologische en bodemkundige kaarten, die een overzicht verschaffen van de verspreiding van de verschillende bosgezelschappen en van hun onderlinge vermengingen, alsmede van de wisselende groeiplaatsomstandigheden. De tabellen van de gezelschappen kunnen inlichting geven over de plaatselijk voorkomende boom- en struiksoorten, alsmede over de percentages, waarmede deze houtsoorten in de gezelschappen optreden.

Met deze gegevens kan de bosbouwer, geheel in overeenstemming met de samenstelling van het ter plaatse thuis horende bosgezelschap, zijn houtsoortenkeuze bepalen voor ieder gedeelte van de reservaten. Bij het inplanten of het inzaaien van de voor een hervorming in aanmerking komende bosgedeelten, zal de bodem zo min mogelijk mogen worden bewerkt (nooit volle grondbewerking), terwijl de bosverjonging nimmer over grote aaneensluitende oppervlakten mag plaats vinden. Velling zal slechts door uitkap mogen geschieden. De voor de ontsluiting benodigde boswegen dienen steeds op een veilige afstand om die plaatsen heen te worden geleid, waar een bijzonder interessante en gevoelige flora en fauna aanwezig is. Voorts verdient het aanbeveling om terreinen aan te wijzen, die zonder bosbouwkundige ingrepen geheel aan de natuur worden overgelaten.

W. van Zeist: Enige absolute dateringen van een veenprofiel uit Zuidoost-Drente.

Van een palynologisch onderzocht veenprofiel bij Emmererfscheidenveen werd op het Fysisch Laboratorium der R.U. te Groningen een aantal monsters volgens de radio-actieve koolstof-methode gedateerd. De resultaten van deze metingen zijn de volgende:

Grens Preboreaal/Boreaal (toeneming van *Corylus*)	6675 ± 180 v. Chr.
Grens Boraal/Atlanticum (*Pinus/Alnus* kruising) . . .	5130 ± 210 v. Chr.
Grens Atlanticum/Subboreaal (daling *Ulmus* curve) . .	3010 ± 135 v. Chr.
Stijging van de *Plantago* curve	2230 ± 140 v. Chr.
Aanvang van de 1% Faguscurve	1395 ± 140 v. Chr.
Laatste *Corylus* maximum	1130 ± 150 v. Chr.

Monster vlak onder het begin van de *Fagus*stijging . . 815 ± 140 v. Chr.
Monster vlak boven het begin van de *Fagus*stijging . . 645 ± 140 v. Chr.

Eveneens werden enige dateringen gegeven van de veenafzetting uit het Eemien bij De Voorst (Noordoostpolder). Deze afzetting behoort tot het eerste gedeelte van het Eemien. Volgens de resultaten van de ^{14}C-methode moet het eerste gedeelte van het Eemien 40.000 tot 45.000 jaar oud zijn. Dit is veel jonger dan tot nu toe verondersteld werd.

A.W.H. Damman: Een nieuwe indeling van de heidegezelschappen.

De kruidlaag van het *Calluneto-Genistetum* wordt volledig beheerst door *Calluna vulgaris*, behalve deze soort komen ook *Agrostis canina*, *Festuca ovina*, *Carex pilulifera* en *Rumex acetosella* nog vrij regelmatig in de heiden voor. Wanneer echter een dichte moslaag aanwezig is verdwijnen ook deze soorten. De beide *Genista*-soorten, *Genista pilosa* en *G. anglica*, ontbreken in de meeste Nederlandse heidevegetaties, ondanks dat de vegetatie zijn naam hier deels aan ontleent.

Bij een nadere bestudering van het *Calluneto-Genistetum* bleek de indeling, die Tüxen in 1937 ontworpen heeft, niet meer in alle opzichten te voldoen. Op grond van gegevens, die bij dit onderzoek werden verkregen, stellen we voor het *Calluneto-Genistetum* te verdelen in vier subassociaties, te weten: een typische subassociatie, waarin verdere diff. soorten ontbreken, een subassociatie van *Genista pilosa*, (Diff. soorten: *Genista pilosa*, *G. anglica*, *Hieracium umbellatum* en *Potentilla erecta*) een orchideeënrijke subassociatie (Diemont 1937) (Vele diff. soorten waaronder: *Pedicularis silvatica*, *Orchis maculata*, *Planthanthera bifolia*, *Gentiana pneumonanthe*, *Galium saxatile* e.a.) en een vierde subassociatie van *Empetrum nigrum* (Tx. 1937), deze laatste is meer geografisch bepaald en komt voor in het noorden van het land.

De typische subassociatie is beperkt tot de armste zandgronden. De subassociatie van *Genista pilosa* ontwikkelt zich op de voedselrijkere of leemhoudende zandgronden. De orchideeënrijke subassociatie komt voor op leemgronden met een behoorlijke ontwatering, bovendien is brand of beweiding noodzakelijk voor het in stand houden van deze vegetatie.

De vegetaties, die vroeger tot het *Calluneto-Genistetum molinietosum* gerekend werden, kunnen nu beter als vochtige varianten van de diverse subassociaties worden beschouwd. Er zijn verschillende redenen om de associatie in eerste instantie naar voedselrijkdom van de grond in te delen en vervolgens pas naar het vochtgehalte.

In verband met het ontbreken van de *Genista*-soorten in de voedselarme heiden, die het overgrote deel van ons heideareaal in beslag nemen, zou het beter zijn van *Callunetum* te spreken i.p.v. *Calluneto-Genistetum*.

De verschillende subassociaties kunnen nog in meerdere varianten worden onderverdeeld. Zo blijkt op opgestoven, voedselrijkere koppen in de heide een variant van het *Callunetum genistetosum* voor te komen met als diff. soorten: *Thymus serpyllum*, *Arnica montana*, *Hieracium pilosella* en *Hypochoeris radicata*. *Hieracium umbellatum* heeft in deze variant zijn optimum.

Van de vele *Cladonia*-soorten bleek geen enkele soort specifiek voor een bepaald type, wel was de abundantie van de *Cladonia*-soorten groter in de arme heidevegetaties. Een aantal hogere planten zoals *Carex pilulifera*, *Festuca ovina*, *Agrostis canina* en *Sieglingia decum*-

bens bleken daarentegen meer voor te komen in het *Callunetum genistetosum* en het *Callunetum orchidetosum* dan in het *Callunetum typicum*.

Ir F.M. Maas: Samenstelling en synoecologie van bronvegetaties.

Uit gegevens van Thienemann, Roll e.a. over bronnen in Duitsland en uit de resultaten van eigen metingen in de brongebieden van de Hemelse Berg te Oosterbeek, de Paasberg te Arnhem, Middagten e.a. is gebleken, dat twee milieufactoren bepalend zijn voor de bronvegetaties, nl. de constante watertemperatuur (9 à 10°C) en het constant hoge zuurstofgehalte van het bronwater. 's Zomers zijn de bronnen dus koud, 's winters daarentegen juist warm. Dit laatste heeft tot gevolg, dat vrijwel alle planten ook in de winter blijven assimileren en dan een groene oase vormen tussen sneeuw en ijs. Ook de vogelwereld is hier dan geconcentreerd. Vroeg in het voorjaar kunnen de planten hierdoor al bloemen vormen; b.v. de goudveilsoorten, het speenkruid, anemonen, dotters en pinksterbloemen, en dat terwijl de omgeving dan nog dor is.

Onder invloed van het voedselgehalte en de stroomsnelheid van het water, het licht en de afstand tot de bronnen treden verschillen op in de vegetatie, b.v. het *Cardaminetum amarae* in lichte, rijke bronnen, het *Caricetum remotae* in donkere, iets armere bronnen en de gemeenschap van *Montia rivularis* en *Philonotis fontana* in open bronbeken, met sterker wisselende temperaturen en een hoger zuurstofgehalte.

De Klasse der brongemeenschappen, *Montio-Cardaminetea*, met o.a. de nieuwe kensoorten *Epilobium obscurum* en *Chiloscyphus rivularis*, moet nieuw ingedeeld worden, nl. in twee verbonden: een *Montion*, waartoe de *Montia*vegetaties in de bronbeken behoren, en een *Cardamineto-Chrysosplenion* met de typische brongemeenschappen *Cardaminetum amarae* en *Caricetum remotae*. Mozaieken hiervan met bosvegetaties komen dan in de bronbossen voor, nl. op zware, rijke bodem *Alnetum glutinosae cardaminetosum* (overgaand in *Pruneto-Fraxinetum)* en op zanderige, iets armere bodem *Alnetum glutinosae caricetosum remotae* en *Cariceto remotae-Fraxinetum* (overgaand in *Quercion-* en *Carpinion*-vegetaties).

H. Doing Kraft: De tegenwoordige opvattingen omtrent het associatiebegrip en de systematiek van plantengezelschappen volgens de methode van Braun-Blanquet.

Wanneer men de „scholen" in de vegetatiekunde slechts opvat als verschillende werkmethoden, waaraan men de omstandigheden, waaronder ze ontstonden, nog kan herkennen, blijkt het, dat veel van wat vroeger met elkaar in strijd werd geacht, gelijktijdig toegepast kan worden. Dit is zelfs mogelijk met behoud van het hierarchisch systeem van associaties, verbonden enz. van Braun-Blanquet en zijn leerlingen en geestverwanten. Dit is in overeenstemming met het feit, dat in dit systeem de „kensoorten" als voornaamste criterium voor het onderscheiden van eenheden reeds sinds langere tijd en in steeds sterker mate voor een belangrijk deel worden vervangen door de differentierende soorten. Verdedigd werd, dat men de kensoort kan opvatten als een speciaal geval van de differentierende soort. Voorts wordt ook steeds meer aandacht besteed aan de geografische differentiatie (die vaak aanleiding kan geven tot het onderscheiden van

„associatie-groepen" als speciale eenheden binnen de verbonden), en aan de dominantie van bepaalde levensvormen (waarbij men b.v. gebruik kan maken van formaties). Ook in verband met de oecologische (b.v. geomorfologische) differentiatie bleek het vaak wenselijk, de bestaande floristische verschillen tot uitdrukking te brengen in het onderscheiden van een groter aantal associaties, waarbij het opvalt, dat de climaxbossen floristisch vaak weinig kenmerkende soorten bevatten, en de aan meer extreme milieus gebonden associaties vaak vele. Voor het tot stand komen van een associatie is een bepaalde duur van stabiliteit van het milieu vereist (die voor elke associatie een eigen waarde heeft), en bovendien een bepaald soortenaantal (bepaalde soortengroepen moeten aanwezig zijn, om invoeging in het systeem mogelijk te maken). Is aan deze eisen niet voldaan, dan heeft men te maken met successietypen resp. met sociaties of consociaties. Dit zijn dus eenheden, die men gedwongen is, nog naast de associaties (en de overgangen daartussen) te onderscheiden, omdat zij niet in het systeem daarvan passen. De overige vegetatie moet geheel opgedeeld worden tussen de associaties, ook indien men daardoor een aantal associaties zonder kensoorten verkrijgt. Bepalend is vooral de grootte der floristische verschillen in het algemeen. Men moet zich ervoor hoeden, soortenarme vegetatietypen reeds bij voorbaat als onvolwaardig aan te zien. Als maat voor de eisen, waaraan een associatie moet voldoen, kan men gebruik maken van een aantal „klassieke" associaties, die reeds lange tijd algemeen erkend zijn als zodanig, zonder dat de inhoud ervan wezenlijk anders wordt opgevat, dan oorspronkelijk was bedoeld, en die voldoen aan de „orthodoxe" eis van de aanwezigheid van kensoorten. Ter wille van de vergelijkbaarheid dient men op alle niveaux van sociologische progressie over dergelijke associaties te beschikken, hetgeen in Nederland ook het geval is.

COMMISSIE VOOR DE PLANTENFYSIOLOGIE

Dr R.J. Helder: Opname en verdeling van gemerkt fosfaat bij jonge gerstplanten.

Gerst planten werden gebruikt, die, op Hoagland oplossing opgekweekt, het tweede blad stadium hadden bereikt. Een dag voor de proef werden 8 series, elk van 12 planten samengesteld en bij constante temperatuur en belichting op geäereerde Hoagland oplossing geplaatst. Er mag dus worden aangenomen, dat de snelheden van de verschillende opname en transport processen zich op een constant niveau hebben ingesteld.

Bij de eigenlijke proef werd de oplossing vervangen door een van dezelfde samenstelling, doch waarvan het P door het toedienen van radioactief P was gemerkt. Op de principes van het merken en op enige technische details werd kort ingegaan.

Daar voor de plant alle omstandigheden dezelfde blijven mag men verwachten dat het P-gehalte met constante snelheid blijft stijgen. Let men echter alleen op het gemerkte P, dan blijkt dit aanvankelijk zeer sterk toe te nemen. De snelheid van toename daalt geleidelijk om na 2 uur constant te worden.

Dit verloop kan verklaard worden door aan te nemen dat in de wortels een hoeveelheid P aanwezig is die gemakkelijk uitgewisseld kan worden tegen het P in het milieu. Wanneer bovendien wordt aangenomen dat deze mobiele fractie tevens dient als reservoir, waar de wortel zelf en de spruit hun P uit betrekken, dan is het mogelijk de grootte van deze mobiele fractie, de totale influx en gelijktijdige efflux, de snelheid van fixatie in de wortel en de doorvoer naar de spruit te bepalen. Met behulp van deze gegevens is het dan mogelijk het verloop van het gehalte aan gemerkt P in wortel en spruit te berekenen.

Bij proeven die langer duren dan 8-10 uur, ziet men vaak, dat de toename aan gemerkt P in de spruit afneemt. Uit nadere analyse blijkt dat dit geheel of ten dele berust op een gelijktijdige terugvoer naar de wortel. Deze afvoer blijkt gemakkelijk 20-30% van de aanvoer te kunnen bedragen. Onder bepaalde omstandigheden kan er dus een indrukwekkende circulatie van P in de plant optreden. De consequenties hiervan voor de verdeling en herverdeling van het P werden kort aangegeven en door de resultaten van een proef geïllustreerd.

Gememoreerd werd dat dit onderzoek financieel wordt gesteund door Z.W.O.

Dr W.K.H. Karstens (mede namens Mevr. V. de Meester-Manger Cats en J.J. Gottenbos): Groei en ontwikkeling van plantenweefsels in vitro met zetmeel als koolstofbron.

Het eerste colloquium over de fysiologie van plantaardige weefselkweken te Briancon van 14-21 juli 1954 gehouden heeft uitgewezen, dat onderzoek naar voor weefselkweken vereiste voedingsstoffen een uitermate grote plaats inneemt in het hedendaagse weefselkweekonderzoek. Hierbij staat de vraag, wat voor voedingsstoffen moeten het weefsel worden aangeboden ten einde goede groei te krijgen, op het eerste plan; de vraag, wat gebeurt er in de voedingsbodem onder invloed van het gekweekte weefsel, is echter nooit gesteld.

Behalve een aantal anorganische bestanddelen, een enkel aminozuur en vitamine is een koolstofbron noodzakelijk om groei te verkrijgen. Hiervoor wordt meestal glucose, ook wel saccharose, gebruikt, terwijl ook enkele andere koolstofbronnen op hun bruikbaarheid zijn onderzocht en minder geschikt of zelfs ongeschikt werden bevonden.

Het leek ons, dat een onderzoek naar de mogelijkheid tot gebruik van zetmeel als koolstofbron iets zou kunnen leren over de invloed van de weefselkweek op de voedingsbodem. In de literatuur is over het gebruik van zetmeel als koolstofbron weinig te vinden. Gautheret en Riker met zijn medewerkers hebben zetmeel gebruikt en waargenomen, dat de groei hierop slecht of matig is. Van voortgezette cultuur op zetmeelbodems is bij deze auteurs niets te vinden.

Anders staat het met het werk van Nickell en medewerkers, dat ons eerst bekend werd tijdens het genoemde colloquium. Als uitgangsmateriaal gebruikten zij virus-tumoren, die op wortels van *Rumex acetosa* voorkomen. De hiervan afgeleide stam bleek goed op zetmeelhoudende bodems te groeien en is reeds vele malen overgeënt.

Intussen hadden we in Leiden een aantal stammen onderzocht op hun vermogen om zetmeel als koolstofbron te gebruiken. Een tweetal stammen bleek geschikt, een crown-gall stam van *Nicotiana tabacum* en een cambiumstam van *Rubus fruticosus*. Van de eerste zijn twee zetmeelstammen afgeleid, thans resp. in hun 8e en 7e overenting, terwijl die van de *Rubus*-stam afkomstig thans in de 6e overenting is.

Het is duidelijk, dat, wil zetmeel door een in vitro gekweekt weefsel als koolstofbron gebruikt kunnen worden, dit door het weefsel in kwestie in een opneembare vorm moet worden omgezet. Dit gebeurt inderdaad en wel door amylasen.

Brakke en Nickell merkten op, dat het bij het *Rumex*-weefsel uitsluitend om α-amylase ging, terwijl in ons laboratorium werd gevonden, dat in de beide onderzochte gevallen zowel α- als β-amylase in het spel zijn.

Een voor de hand liggende vraag is, of er sprake is van actieve enzymadaptatie. Dit is niet het geval. Voor het *Rumex*-weefsel werd aangetoond, dat evenveel amylase gevormd wordt, of nu glucose dan wel zetmeel als koolstofbron wordt aangeboden. Ook voor de door ons onderzochte gevallen scheiden glucose-cultures amylasen af, terwijl bovendien opgemerkt werd, dat de groeisnelheid bij voortgaande overenting op zetmeelbodem niet groter werd.

Een tweede vraag is op welke wijze de betrokken enzymen in de voedingsbodem terecht komen. Nickell meent, dat het een actieve uitscheiding is, Gautheret gaf gedurende het colloquium als zijn mening te kennen, dat in een weefselkweek door de groei bepaalde cellen in het gedrang komen en de celinhoud in contact met de voedingsbodem komt.

Het is opvallend, dat de zetmeelcultures van *Nicotiana* en *Rumex* van meet af aan er geheel anders uitzien dan glucose cultures.

Nicotiana-weefsel op glucose gekweekt vormt halfbolvormige, compacte, witte cultures, op zetmeelbodem is de structuur veel losser, waterig van consistentie en groen van kleur. Ook de *Rubus*-cultures op zetmeel zijn veel losser van bouw, maar, terwijl hier juist de glucose cultuur groen is, is die op zetmeel bleekgeel.

Van de inwendige structuur, en dit geldt speciaal voor *Nicotiana*, valt ook het een en ander te vermelden. Op glucose gekweekt is een grote activiteit van geïsoleerde secundaire meristemen, sterk ontwikkelde phloeem- en xyleem-gebieden opleverend, waar te nemen. Deze activiteit is bij de zetmeelcultures opvallend gering, waardoor slechts enkele phloeem- en xyleem-gebiedjes gevormd worden en de rest van de cultuur uit los parenchymatisch weefsel bestaat. Bij de glucosecultuur wordt dit parenchymatische weefsel door de zich uitdijende phloeem- en xyleem-gebieden in sterke mate verdrukt.

De waargenomen veranderingen zijn niet gefixeerd. Teruggeënt op glucose komt de typische glucose-cultuurvorm met de daarbij behorende inwendige structuur reeds in de eerste terugenting weer te voorschijn.

Dr J. Venekamp: Over de vorming en betekenis van het asparagine in geëtioleerde kiemplanten van *Lupinus luteus*.

Hoewel het asparagine reeds in 1806 ontdekt werd en sindsdien sterk de aandacht van talrijke onderzoekers heeft getrokken, stelden Dunn en medewerkers zich de vraag, welke aminozuren van het eiwit bijdragen aan de asparaginevorming bij geëtioleerde, op water gekweekte kiemplanten van *Lupinus lutens*. Langs microbiologische weg bepaalden zij de concentraties van 12 aminozuren, waardoor dit onderzoek niet zo volledig was als gewenst is. Daarom werd door ons getracht, zoveel mogelijk alle aminozuren in het onderzoek te betrekken. De omstandigheden, waaronder de lupine gekweekt werd, waren dezelfde als bij het onderzoek van Dunn. Voor de analysen werden monsters van 100 zaden en van kiemplanten van 7,14 en 21 dagen oud genomen.

Door de zaden of kiemplanten in aether of alcohol te vermalen en de suspensies in een zuil te gieten, werden de vrije amiden en aminozuren door percolatie met 70% alcohol uit het weefsel geëlueerd en daarna de eiwitten gedeeltelijk gehydrolyseerd door percolatie met 6n HCl, waarbij de ontstane producten oplosten. Ten slotte werden de nog niet opgeloste eiwitresten in oplossing gebracht door percolatie met 6n HCl, dat door een kokende watermantel verwarmd werd. Na verwijdering van de koolhydraten en anorganische ionen door percolatie van de extracten door ionen-wisselaars en na volledig hydrolyseren van de oplossingen, welke de eiwitsplitsingsproducten bevatten, werden de aminozuren papierchromatografisch geïdentificeerd en de concentraties bepaald met behulp van de methode volgens Stein en Moore, waarbij zetmeelzuilen gebruikt werden.

Volgens literatuur-opgaven zijn de aminogroepen van de amiden afkomstig van asparaginezuur. Deze stof is aanwezig in het eiwit of wordt gevormd uit glutaminezuur, alanine, leucine, isoleucine, phenylalanine, tyrosine en valine door een transamineringsreactie of uit proline en histidine volgens andere reacties. Onze analysen toonden aan, dat in de kiemplanten deze aminozuren als bron voor de aminogroepen fungeerden. Hetzelfde was het geval met de amide-groepen, welke afkomstig zijn van ammonia, glycine, serine, cystine, lysine, α-aminoadipinezuur, threonine, histidine en arginine.

Volgens verschillende onderzoekingen wordt 1 Mol. arginine afgeleid van 2 Mol. glutaminezuur, 1 Mol. asparaginezuur en 1 Mol. ammoniak. Bij de afbraak geeft 1 Mol. arginine met 1 Mol. α-ketoglutaarzuur aanleiding tot de vorming van 2 Mol. glutaminezuur en 2 Mol. ammoniak. Ook dit werd door onze analysen bevestigd.

De aminozuren kunnen wij verdelen in een groep van stoffen, welke omgezet worden tot producten, welke verwant zijn aan pyrodruivenzuur, zoals leucine, isoleucine, valine, alanine, serine, glycine en cystine en een groep van verbindingen, welke al of niet na transaminering oxaalazijnzuur of α-ketoglutaarzuur vormen, waaruit de amiden ontstaan (asparaginezuur, glutaminezuur, arginine, proline, histidine, α-aminoadipinezuur, lysine en threonine). Tyrosine en phenylalanine behoren tot beide groepen. Inderdaad bleek uit onze analysen, dat de toename in de hoeveelheden asparagine, glutamine en arginine correspondeerde met de afname van phenylalanine, tyrosine en de aminozuren van de tweede groep. De hoeveelheden oxaalazijnzuur, omgezet is asparagine, en α-ketoglutaarzuur, afgebroken tot oxaalazijnzuur, konden berekend worden. Na deze berekeningen kon de balans gemaakt worden van de verbindingen, welke aanleiding geven tot de vorming van α-ketoglutaarzuur en van de stoffen, die van α-ketoglutaarzuur afgeleid kunnen worden.

In geëtioleerde kiemplanten worden eiwitten verademd.

Hierbij worden de aminozuren van de eerste groep geoxydeerd, waarbij ammoniak vrijkomt, dat de Krebs-cyclus remt. Uit de aminozuren van de tweede groep ontstaat meer katalytisch oxaalazijnzuur. Daar deze niet verder geoxydeerd wordt, is dit de enige stof, welke ammoniak bindt, zodat na transaminering asparagine als eindproduct van de eiwitademhaling wordt gevormd.

Ir J.A.D. Zeevaart, mede namens Dr Ir J.A.J. Stolwijk: Bloei van *Hyoscyamus niger* in licht van verschillende spectraalgebieden.

Het besproken onderzoek werd verricht in een opstelling op het Laboratorium voor plantenfysiologisch onderzoek te Wageningen, waarmee het mogelijk is planten onder geconditioneerde omstandigheden op te kweken in licht van nauw begrensde spectraalgebieden, zonder ze aan wit licht bloot te stellen. Bij alle vroeger onderzochte planten werd vrijwel geen verschil in het tijdstip van bloei waargenomen, terwijl in groen, geel en rood licht een sterke stengelstrekking optrad, vergeleken met de planten in blauw, violet en wit licht.

De lange-dag plant *Hyoscyamus niger* blijkt in lange dag (LD) echter zeer preferent te bloeien in blauw, violet en rood licht, waarin een zekere hoeveelheid infrarood straling voorkomt; 30% infrarood (rode straling op 100% gesteld) had reeds hetzelfde effect als 300% infrarood. In groen, geel en rood licht (dus in het golflengtegebied van 500-700 mμ) bleven de planten echter in LD vegetatief. In dit verband wordt dus het begrip kritieke daglengte (= die daglengte, waarbij nog juist bloei plaats vindt) uiterst relatief.

Ondanks de preferente bloei in blauw-violet-infrarood blijkt een LD echter noodzakelijk te zijn voor de bloei, daar in een 9-urige korte dag in alle kleuren de planten vegetatief bleven.

Uit verdere proeven is gebleken, dat in een 9-urige belichting met blauw licht een toestand wordt opgebouwd, die op zichzelf nog geen bloei geeft; wordt deze 9 uur blauw licht echter aangevuld met 15 uur rood licht, dan vindt snel bloei plaats, terwijl in 24 uur rood licht per dag de planten vegetatief blijven. Zelfs met 9 uur blauw licht en daarna 63 uur rood licht werd nog bloei verkregen. De violet-blauw-infrarood-behoefte is dus niet de enige factor, die tot bloei leidt. Er is nog een aanvullende fotoperiodieke stimulus nodig, die echter zowel door rood als door blauw licht kan worden geleverd.

In de literatuur over fotoperiodiciteit wordt algemeen de hoge lichtintensiteitsreactie geïdentificeerd met de fotosynthese. In onze proeven bleek, dat de planten in rood licht méér droge stof produceerden dan in blauw licht. Dit verschil kan hoofdzakelijk aan een verschillend aantal quanten (gelijke lichtintensiteiten in beide spectraalgebieden) worden toegeschreven. Deze waarneming maakt het echter onwaarschijnlijk, dat bij *Hyoscyamus niger* de hoge lichtintensiteitsreactie uitsluitend bestaat uit fotosynthese.

Literatuur: Stolwijk J.A.J. and J.A.D. Zeevaart; Wavelength dependence of different light reactions governing flowering in Hyoscyamus niger.
Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, C 58, 386-396 (1955).

Dr B. Kok: Een lichtremming van het fotosynthese proces.

Het is sinds lang bekend dat groene plantendelen door overmatig sterk licht beschadigd worden. Dit geldt niet alleen voor bladeren maar ook voor eencellige wieren. Zoals tussen schaduw- en lichtplanten, bestaan ook bij algen grote verschillen in gevoeligheid voor deze beschadiging.

Met behulp van een microvolumetrische methode was het mogelijk zeer hoge lichtintensiteiten op algenmateriaal te concentreren en de remming van het fotosynthese proces quantitatief te bestuderen.

Bij toediening van sterk licht blijkt de primaire fotochemische reactie (het quantenrendement) geïnactiveerd te worden in een proces dat volgens eerste orde verloopt en onafhankelijk van de temperatuur is. De halfwaarde tijd van de remming is omgekeerd evenredig met de lichtintensiteit.

De fotosynthetische verzadigingssnelheid begint in de meeste gevallen pas enige tijd na toediening van het sterke licht af te nemen – deze afname volgt dan echter dezelfde wetmatigheden.

Hoewel het niet mogelijk was een volledig werkingsspectrum van de lichtremming te meten, kon worden vastgesteld dat dit spectrum verschilde van het actiespectrum van de fotosynthese; blauw licht was in verhouding sterker werkzaam.

Een directe vernietiging van pigment, zich uitend in een verandering in het absorptiespectrum, kan niet worden geconstateerd. In een (temperatuur afhankelijke) donkerreactie wordt door de cellen de beschadiging betrekkelijk langzaam hersteld.

Samenvattend kan worden geconcludeerd, dat het pigmentcomplex van groene cellen in alle intensiteiten fotochemisch wordt geïnactiveerd en in donkerprocessen weer hersteld. Daar het quantenrendement van de inactivering betrekkelijk laag is, wordt het effect pas in sterk licht manifest.

Dr D. Stegwee: Enige aspecten van de purinestofwisseling bij *Ophiostoma* mutanten.

Uit met UV bestraalde conidiosporensuspensies van de ascomyceet *Ophiostoma multiannulatum* (Hedgc. et Davids) von Arx werden met behulp van een aan Fries ontleende ophopingsmethode fysiologisch afwijkende stammen (mutanten) geïsoleerd. Hieronder bevonden zich een aantal, die van de normale ouderstam afweken in die zin, dat de biosynthese van adenine geblokkeerd was. Deze blokkering lag bij verschillende mutanten op verschillende plaatsen in de reactieketen en kwam tot uiting in de additionele behoefte aan purine-groeistoffen, vertoond door de mutanten. Door vergelijking van deze groeibehoeften, alsmede door een onderzoek naar de ophoping van produkten van de normale biosynthese vóór de blokkering, werd een inzicht verkregen in de volgorde van reacties en reactiecomponenten betrokken bij de synthese van adenine en -derivaten.

Een onderzoek naar de synthese van nucleinezuren bij een adenine-deficiente mutant bracht aan het licht, dat deze synthese veel efficienter verliep, wanneer adenosine-3-fosfaat i.p.v. adenine aan het voedingsmedium werd toegevoegd. Dit werd dan ook als mogelijke oorzaak aangewezen van het verschijnsel, dat adenine-deficiente mutanten met adenosine-3-fosfaat een 2-3 maal zo hoog gewicht aan droge stof bereikten als met adenine.

Als voorlopige conclusie werd een schema voor de nucleinezuursynthese bij *Ophiostoma* voorgesteld, omvattende de volgende verbindingen: glycine, mierenzuur, CO_2, NH_3 en ribose; amino-imidazoolcarboxamide-ribotide; inosine-3-fosfaat; adenosine-3-fosfaat.

Dr J.S.C. Wessels: Nieuwste inzichten in de lichtreactie bij de fotosynthese.

Het fotosyntheseproces is opgebouwd uit een lichtreactie en een serie donkerreacties. De lichtreactie vindt plaats in de chloroplastengrana en leidt tot splitsing van water, waarbij een reducerende verbinding en zuurstof worden gevormd. De donkerreacties hebben vermoedelijk in het stroma der chloroplasten plaats en bestaan uit een reductie van koolzuur, welke uiteindelijk resulteert in de vorming van koolhydraten.

De grana zijn bij belichting, in aanwezigheid van b.v. benzochinon, in staat zuurstof te produceren, onder gelijktijdige reductie van chinon tot hydrochinon. Deze reactie, die in 1937 door Hill werd ontdekt, wordt de Hill-reactie genoemd. De Hill-reactie heeft met de fotosynthese de lichtreactie, dus de fotochemische splitsing van water, gemeenschappelijk, doch in plaats van koolzuur treedt hierbij het chinon als waterstofacceptor op. De Hill-reactie kan o.a. worden bestudeerd door meting van de redoxpotentiaal. Aangezien naast fotoreductie foto-oxydatie van het gevormde hydrochinon door zuurstof optreedt, welke door chlorofyll blijkt te worden gesensibiliseerd, is het noodzakelijk de metingen in stikstofatmosfeer uit te voeren.

Het blijkt dat chloroplastengrana bij belichting uitsluitend chinonen en kleurstoffen met een betrekkelijk hoge normaalpotentiaal kunnen reduceren. De laagst bereikbare potentiaal bedraagt bij pH 6,5 ongeveer 0 mV. Dit is in overeenstemming met het feit dat de energie van een door chlorofyll geabsorbeerd rood lichtquant te gering is om redoxstoffen met een normaalpotentiaal beneden 0 mV in voldoende mate te reduceren. Men kan hieruit concluderen dat de normaalpotentiaal van de in de grana gevormde reducerende verbinding (XH_2) ongeveer 0 mV bedraagt. Langs indirecte weg kon evenwel worden aangetoond, dat chloroplasten bij belichting in staat zijn DPN te reduceren. Wanneer men n.l. chloroplasten belicht in aanwezigheid van DPN, pyrodruivenzuur en het enzym melkzuurdehydrogenase treedt naast zuurstofontwikkeling reductie van pyrodruivenzuur tot melkzuur op. Aangezien de normaalpotentiaal van DPN – 320 mV bedraagt, moet een directe reductie van deze stof zeer onwaarschijnlijk worden geacht. We moeten daarom aannemen dat bij de reductie van DPN behalve lichtenergie ook nog fosfaatenergie wordt gebruikt. De benodigde energie-rijke fosfaatbanden kunnen ontstaan door reoxydatie van een deel der primair gevormde XH_2-moleculen. Dit suggereert dat X een schakel is in het proces van oxydatieve fosforylering. Vitamine K, dat sinds kort als een intermediair van dit proces bekend is, voldoet tevens aan de voorwaarde dat zijn normaalpotentiaal ongeveer 0 mV bedraagt (n.l. - 25 mV). Op grond hiervan werd de hypothese opgesteld dat dit vitamine een rol speelt bij de waterstofoverdracht in de Hill-reactie, m.a.w. identiek is met de stof X. Een steun voor deze hypothese vormt o.a. het feit dat antagonisten van vitamine K, zoals dicumarol, de Hill-reactie in sterke mate blijken te remmen.

Het chlorofyll bevindt zich in de grana in het grensvlak tussen de eiwit- en lipoidlagen, met de fytylzijketen in de lipoidlaag. Aangenomen wordt nu dat associatie door middel van waterstofbruggen optreedt tussen de cyclopentanonring van chlorofyll en vitamine K, welke binding wordt versterkt doordat ook vitamine K, dat evenals chlorofyll is opgebouwd uit een hydrofiel gedeelte en een lipofiele fytylrest, in het grensvlak tussen de eiwit- en lipoidlagen is georienteerd. Bij belichting zou een electronenoverdracht van chlorofyll naar vitamine K kunnen optreden, waardoor dit vitamine in de gereduceerde vorm overgaat.

De werking van een aantal remstoffen van de Hill-reactie kan met behulp van deze hypothese plausibel worden gemaakt. Zo zou bv. fenylurethaan kunnen associeren met de cyclopentanonring van chlorofyll, waardoor de energieoverdracht van chlorofyll naar vitamine K wordt belemmerd. In overeenstemming met deze opvatting blijken fenylureumderivaten, zoals b.v. het als herbicide bekende CMU, de Hill-reactie in aanzienlijk sterkere mate te remmen dan fenylurethaan.

Dr P. Massini: Tracer-onderzoek in de fotosynthese.

De methode van radioactieve tracers werd toegepast op het probleem van de weg van het koolstofatoom van het koolzuur in de fotosynthese (Calvin en medewerkers 1), 2)). Daarbij wordt aan een suspensie van groene eencellige algen (b.v. *Chlorella, Scenedesmus)* in het licht radioactief koolzuur toegediend. Na een korte tijd worden de algen in kokende alcohol gedood en geëxtraheerd. Het bleek dat na tijden van een minuut of minder de radioactief geworden verbindingen vrijwel volledig in alcohol oplosbaar zijn. Het extract wordt geconcentreerd en aan de tweedimensionale papierchromatographie onderworpen. Met het chromatogram wordt een rōntgenfilm in contact gebracht. Na een of meer weken vertoont de ontwikkelde film een zwarting op die plaatsen, waar het chromatogram een radioactieve stof bevat. De stof kan worden geidentificeerd door vergelijking van zijn chromatografische coördinaten met die van bekende stoffen.

Met deze methode kon worden aangetoond dat het eerste stabiele carboxyleringsproduct van de fotosynthese fosfoglycerinezuur is. Deze stof wordt door coënzym I, met behulp van ATP, gereduceerd tot fosfoglycerinealdehyde, dat gedeeltelijk langs de weg van de glycolyse in hexose en zijn polysacchariden omgezet wordt.

Het gereduceerde coënzym wordt geleverd door de eigenlijke lichtreactie, waarin water met behulp van chlorofyll gesplitst wordt in een geoxydeerd en een gereduceerd gedeelte. Ook de energie voor de ATP-vorming wordt waarschijnlijk door de lichtreactie geleverd. Een deel van het gevormde triosefosfaat wordt echter in een reeks reacties, die door verschillende transaldolasen en transketolasen gekatalyseerd worden, omgezet in ribulosefosfaat, een C_5-keto-suiker-fosfaat, dat door ATP in difosfaat omgezet wordt. Het ribulosedifosfaat wordt tenslotte gesplitst onder CO_2-opname in 2 moleculen fosfoglycerinezuur. We hebben dus te maken met een kringloop waarin CO_2, met behulp van ATP en gereduceerd coënzym I, wordt omgezet in (hoofdzakelijk) hexosefosfaat.

1) M. Calvin, A.A. Benson, Science 109, 140 (1949).
2) J.A. Bassham et.al., J. Amer. Chem. Soc. 76, 1760 (1954).

G. Meijer: Invloed van rood en blauw licht op de plantengroei.

Planten, opgekweekt in licht van verschillende golflengten, vertonen grote verschillen in ontwikkeling. In rood licht ontwikkelen zich lange, in blauw licht korte internodiën.

Bij de meeste planten treedt in rood licht epinastie op, bij *Hyoscyamus niger* vonden Stolwijk en Zeevaart echter juist in het kortgolvige licht epinastie. Bij de tomaat is de bladlengte in rood groter dan in blauw licht; bij *Mirabilis jalapa* treedt juist het omgekeerde op. Blauw licht veroorzaakt anthocyaanvorming o.a. bij *Coleus* en appels. *Rivina* en *Acer* groeien in blauw licht normaal, in rood licht worden de bladeren geel en de planten sterven af.

Vervangt men een of meer uren van een 16-urige belichting/dag met rood licht (16R) door blauw licht, dan blijkt het grootste effect (internodiën- en bladlengten) op te treden tot en met 3 uur blauw (13R 3B). Bij 8R8B verkrijgt men al een habitus welke hetzelfde is als die bij 16 uur blauw licht/dag (16B).

Bij verschillende planten vinden we een snellere bloei in rood licht, welke niet veroorzaakt wordt door een beinvloeding van een bloemaanleg, maar door een sneller uitgroeien van de internodiën. Bijv. bij tomaat (dagneutraal) en *Matricaria* (lange dag (LD.) plant).

Kalanchoë, Poinsettia en *Salvia occidentalis* (K.D. planten) bloeien in rood en blauw licht gelijktijdig, mits een korte dag (K.D.) gegeven wordt.

Bij *Kalanchoë* echter bleek een K.D. behandeling (10 uur licht/dag) van 5 weken in rood licht onvoldoende te zijn voor bloemaanleg; dezelfde behandeling in blauw licht leidt echter wel tot bloemaanleg. Bij *Hyoscyamus* vond Stolwijk (1955) een vertraagde bloemaanleg in rood licht. *Salvia occidentalis* (K.D.) vertoont, hoewel in rood licht in korte dag normaal bloeiend, een vegetatieve tendens, d.i. de zijtakken staan verticaal zoals bij vegetatieve planten in L.D. Bij planten in K.D., welke dus generatief zijn, groeien de zijtakken horizontaal uit.

De wortelontwikkeling is bij de tomaat in 16R en 16B gelijk, evenwel worden op de onderste internodiën in 16R wèl, in 16B geen adventief wortels gevormd.

Bij *Coleus* stekken bleken zowel in 16R als in 16B wortels langs het wondvlak gevormd te worden; langs de stengel echter is het uitgroeien van wortels in 16B geremd t.o.v. 16R. Bij *Mirabilis jalapa* wordt in 16B een verdikte penwortel gevormd, in rood licht niet. Hoewel bij erwten geen verschil in drooggewicht te vinden is, is de hoofdwortel in 16R tweemaal zo lang als in 16B.

Verschillende van de hier genoemde effecten, zoals epinastie, wortelvorming en beinvloeding van de bloei bij Kalanchoë zijn ook door een behandeling met groeistof te verkrijgen. Dit geldt ook voor het sterkere spiraliseren van Vallesneria-bladeren in rood licht.

De vraag, of het hier een beïnvloeding van het groeistofgehalte, dan wel van de gevoeligheid voor groeistof betreft, moet nog onbeantwoord blijven.

COMMISSIE VOOR DE PLANTENSYSTEMATIEK

A.C. van Bruggen: Problemen bij de bewerking van het geslacht *Payena* A.DC (Sapotaceae)

Het grondtype van de bloem der Sapotaceae – Madhucoideae – Madhuceae is in principe S 4, P 8, A 16, G 8. Deze tribus omvat de genera *Ganua*, *Burckella* (beide al recent voor de Flora Malesiana bewerkt, *Madhuca* en *Payena*. De variatie op de grondformule van de bloem is bij *Payena* het geringst; volgens de literatuur S 4, P 6-8, A 12-20, G 6-8.

De calyx bestaat uit twee kransen van twee (binnen imbricaat, buiten valvaat). Bij de corolla werden nog geen variaties gevonden; de dekking van de lobben vertoont een toevallige imbricatie. De 16 meeldraden staan in twee min of meer duidelijke kransen van 8. Het gynaecium, dat een priemvormige stijl draagt, bevat 8 uniovulate loculi. Bij het getal van de stamina en de loculi werden nog geen afwijkingen gevonden, behalve bij het type van *Payena annamensis* (Indochina) waar 6-8 hokjes gevonden werden. *Payena* staat hier echter aan de rand van zijn areaal, zodat een afwijking hier verwacht zou kunnen worden. De vrucht bevat één of twee zaden met een dunne testa en een duidelijk litteken. Dikwijls variëren de afmetingen van zaad en litteken sterk binnen de soort. Het meest essentiële van het zaad is het al of niet aanwezig zijn van endosperm. *Payena* heeft n.l. rijkelijk endosperm en *Madhuca* slechts een dun membraneus laagje hiervan. De cotylen zijn derhalve bij *Payena* dun, bij *Madhuca* dik (parallellen komen o.a. voor bij de subfamilie Sideroxyloideae). Van de bladen zijn vooral de nervatuur en de beharing van belang. Eén soort is geheel dicht wollig behaard, takken, stengels van blad en bloem, kelk en blad dragen een dicht indumentum. Ook hier is een parallel en wel bij het verwante geslacht *Ganua*.

Het areaal van *Payena* strekt zich uit van de Philippijnen via Borneo, Java, Sumatra en Malakka tot in Annam. De westgrens ligt ongeveer in Tenasserim; een vindplaats van de Andamanen is bekend. De meeste soorten vindt men op Sumatra en het schiereiland van Malakka; mogelijk ontstond dit genus in het pleistoceen in deze hoek van het Soendaplat. De verwante genera zijn verspreid van India tot de Samoa-eilanden toe.

Voorlopig zijn slechts twee nieuwe soorten van *Payena* gevonden, waarvan één van de bekende berg Kinabalu in Brits-Noord-Borneo. Dit blijkt toevallig de soort met de grootste bladen, bloemen en vruchten van het gehele geslacht te zijn.

Tenslotte zij er op gewezen, dat ten tijde van de voordracht het onderzoek nog niet voltooid was, zodat de mogelijkheid bestaat, dat iets van hetgeen hier geschreven is, bij het beschouwen van meer materiaal geen stand kan houden. De publikatie zal te zijner tijd in Blumea verschijnen.

A.M.W. Mennega: Enkele opmerkingen over het herkennen van bomen in het Surinaamse bos op de stam.

Het herkennen van de bomen in een tropisch regenwoud met zijn zo gevarieerde vegetatie, waarvan de bladeren en bloemen meestal onbereikbaar hoog in een wirwar van takken verborgen zijn, levert steeds vele moeilijkheden. Het ligt dan ook voor de hand dat diegenen die zich bezig houden met bosinventarisatie of op zoek zijn naar waardevolle houtsoorten, andere middelen tot herkennen moeten gebruiken dan de botanicus.

Het meest opvallend zijn de stammen en de inlandse boomkenners herkennen de bomen dan ook grotendeels op een combinatie van kenmerken die de stam en het bastkapvlak opleveren. Het is vaak moeilijk deze kenmerken onder woorden te brengen, maar foto's kunnen daarbij helpen. Op instigatie van Ir I.A. de Hulster en Prof. J. Lanjouw heb ik in Suriname van een aantal voor de Dienst van Lands Bosbeheer belangrijk geachte houtsoorten foto's gemaakt van stamvoet en kapvlak. Het is slechts een oriënterend onderzoek geweest en veel meer foto's en waarnemingen van eenzelfde soort van verschillende ouderdom en van verschillende standplaats zullen nodig zijn om een idee te krijgen van de aspecten die één bepaalde soort kan vertonen.

Aan de hand van een aantal van de vervaardigde foto's is een overzicht gegeven van vormen en stammen (wortelaanzetten, hoog oplopende lijsten, diep gegroefd, steltwortels), van het uiterlijk van de stam (kleur, aanhangsels als stekels en lenticellen, korst, die weer verschillende typen kan vertonen van glad, gegroefd, schilferend, grof bladderend etc.) en van het bastkapvlak (uitstromend sap van witte, rode, gele of beige kleur en verschillende consistentie en smaak, dikte, gelaagdheid, typische dilatatiefiguren, hardheid en kleur). Geur en smaak zijn vaak lastig te beschrijven, maar in bepaalde gevallen zeer kenmerkend (komkommer- en cedergeur, bittere smaak).

J. Heimans: *Viola calaminaria* en *V. alpestris*.

Met behulp van levende planten, gedroogd materiaal, microscopische preparaten, detailfiguren en foto's wordt nog eens de aandacht gevraagd voor de frappante overeenkomst in habitus en in alle andere kenmerken (ook in de variatiebreedte van die kenmerken) tussen het

Zinkviooltje van de Belgische en Nederlandse Geuloevers, en *Viola alpestris* Wittr. (V. *tricolor* L. ssp. *alpestris* Becker) van de subalpine (bovenste naaldhout-) gordel in de Alpen.

Reeds in 1936 heb ik voorgesteld het Zinkviooltje niet meer te betitelen als varieteit van V. *lutea* (V. *lutea* Huds. var. *multicaulis* Koch), maar als een aparte soort te beschouwen (*V. calaminaria* Lej.), het allernaast verwant met *V. tricolor* L. ssp. *alpestris* Becker, die reeds in 1897 door V. Br. Wittrock als aparte soort was afgesplitst van V. *tricolor* s.l. en wel als de oudste stamsoort van de gehele groep, van welke stamsoort zowel *V. tricolor* s.s. als *V. lutea*, *V. arvensis* en *V. calcarata* zouden zijn af te leiden.

Het enige, dat tegen mijn voorstelling scheen te pleiten, was het chromosomengetal, dat voorlopig werd bepaald op ca. 24 (2n = 48), hetzelfde aantal als voor *V. lutea* was vastgesteld, terwijl voor de meeste *V. tricolor*-vormen (zoals *V. alpestris*) n = 13, 2n = 26 werd opgegeven.

Intussen was gebleken, dat het blauwbloeiende Zinkviooltje van Blankenrode in Westfalen n = 26 bezit (Griesinger 1939). Thans is door moeizaam cytologisch onderzoek in het Hugo de Vries-laboratorium geconstateerd, dat *V. alpestris* uit Obergurgl (Toril) n = 13 heeft (prep. R. van Biezen) en *V. calaminaria* van Epen en van Bleijberg (Plombières) n = 26 (prep. Mej. H.N. van den Steenhoven).

Thans verzet zich ook in dit opzicht niets meer tegen de veronderstelling, dat het Zinkviooltje zou zijn een speciaal aan hoog zinkgehalte van de bodem aangepaste tetraploide endemische vorm van *Viola alpestris* Wittr., die wegens separaat areaal, hoge ouderdom en bijzondere milieu-aanpassing de soortsnaam *V. calaminaria* verdient.

Van heel andere kant is nl. nog een argument aan te voeren voor de hoge ouderdom en alpine herkomst van de zinkflora aan de Nederlands-Belgisch-Duitse grens.

Door Jonker (1948) evenals door Van der Hammen (1951) en thans ook in ons Hugo de Vries-laboratorium (B. Zwart n.gepubl.) is nl. pollen van *Armeria* aangetroffen in boormonsters uit het Laat-Glaciaal (zelfs uit de Oudste Toendratijd) van diverse punten in Nederland, o.a. op slechts 30 km ten Noorden van Epen (L.). Het is niet uit te maken of deze pollenkorrels behoren tot *A. Halleri*, zoals onze zinkvorm door K. Schubert (Halle) wordt genoemd. Wel staat vast dat de zeekust in Laatglaciale tijd nog veel verder verwijderd lag dan thans, zodat aan een speciale kustvorm niet behoeft te worden gedacht.

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ERRATUM

Page 556, Fig. 10 left; for:

“HCO_3 9 100 100” read: “HCO_3 900 100 100” curves upwards when it is placed horizontally. The earlier work with this organ mainly concerned the influence of the angle of the coleoptile to the direction of gravity and the influence of external factors, e.g. the estimation of g.t.sin α ($g =$ gravitational force), that is, the minimum time (t) a coleoptile must be kept at a given angle (α) to the vertical in order to obtain a perceptible curvature (RUTTEN-PEKELHARING, 1910); the influence of various temperatures on the presentation time (RUTGERS, 1912) and the geotropic curvature in the absence of free oxygen (VAN AMEYDEN, 1917). Geotropism had mainly been considered from the mechanical point of view, e.g. the theory of HABERLANDT (1900) and NĚMEC (1900) on the statolithic function of starch grains.

After the discovery by DARWIN (1880) that the perception of gravity is localized in the root tip, and the conclusions of ROTHERT (1894) that the same must be true for the coleoptile, and after the remarkable results of BOYSEN-JENSEN (1913), PAÁL (1914, 1919), SÖDING (1923) and WENT (1927, 1928), a new facet of the geotropic reaction was revealed. Particularly by the work of the last-mentioned author it became clear that the tip of the coleoptile is the production centre of a growth-regulating substance and that this growth substance plays a role in the development of the geotropic curvature, which indeed is a manifestation of differential growth.

That growth substance is a necessary factor was clearly shown by the work of WENT (1927). He demonstrated that if gelatine blocks containing growth substance, obtained by diffusion out of *Avena* coleoptile-tips, were placed on decapitated coleoptiles, a geotropic curvature resulted when the coleoptiles were placed horizontally, whereas, when blocks of plain gelatine were placed on the coleoptiles, no curvature occurred. This author, therefore, used a hydro-gel containing growth substance obtained from plant material to induce a geotropic curvature in decapitated coleoptiles. NUERNBERGK (1933) used auxin derived from urine, and found that if it is dissolved in an agar block and in this way supplied to a decapitated coleoptile, the coleoptile curves geotropically. His work therefore indicates that a growth substance, which had not yet been isolated from plant material, can also induce a geotropic curvature. BURKHOLDER (1941) was the first to study the effect of synthetic growth substances (e.g. α-naphthalene-acetic acid, indole-3-propionic acid, indole-3-butyric acid and indole-3-acetic acid) on the geotropic curvature of intact *Avena* seedlings and excised coleoptiles, the growth substances being either dissolved in water or mixed with agar. His conclusion that the growth substances reduce the curvature of the coleoptiles, however, has to be discounted in the light of later work (cf. ANKER 1954) which shows that the concentrations which he used were physiologically either too high or too low. ANKER (1954, 1956) made quantitative studies of the growth-substance requirements of excised, decapitated coleoptiles during the geotropic curvature; in his experiments the growth substances were dissolved in water and the coleoptiles submerged in the solutions. With three different growth substances (indole-3-acetic acid, indole-3-aceto nitrile and α-naphthalene-acetic acid) he demonstrated that the geotropic curvature is maximal in solutions of which the concentrations are sub-optimal for coleoptile growth, and that the geotropic curvature fails to appear in concentrations which are optimal and supra-optimal for coleoptile growth. An important feature of Anker's experiments is that they indicate the possibility of conducting quantitative experiments on geotropism with excised, non-decapitated coleoptiles in water, and with excised, decapitated coleoptiles in solutions of various growth substances.

To explain the differential growth of the upper and lower side in geotropic curvatures, CHOLODNY (1927) and WENT (1927) independently came to the same conclusions. The Cholodny-Went theory of tropisms was formulated in this way: "Growth curvatures, whether induced by internal or external factors, are due to an unequal distribution of auxin between the two sides of the curving organ. In the tropisms induced by light and gravity the unequal distribution is brought about by a transverse polarization of the cells, which results in a lateral transport of the auxin." (WENT and THIMANN, 1937). According to the theory, the auxin concentration on one side of a horizontally placed organ should be higher than on the other side. This view has been corroborated by the following investigations: DOLK (1930, 1936) on the coleoptiles of *Avena* and *Zea mays*; NAVEZ and ROBINSON (1933) on the coleoptile of *Avena*; DIJKMAN (1934) on the hypocotyl of *Lupinus* and VAN DER LAAN (1934) on the epicotyl of *Vicia faba*. Their results all show that the amount of growth substances diffusing from the lower half of the horizontally placed organ is higher than the amount diffusing from the upper half, but the question as to how these differences arise, is still unanswered.

BRAUNER (1926, 1927, 1928) showed that in horizontally placed tissue, living or dead, as well as in a suitable model (two electrolyte solutions separated by parchment paper) a transverse electrical polarity is established. The upper side of a horizontally placed coleoptile becomes electrically negative with respect to the lower side. Brauner called this phenomenon "geo-electric effect". Further investigations on the difference in potential between the upper and lower side of horizontally placed plant organs were carried out by BRAUNER and AMLONG (1933), CLARK (1937) and SCHRANK (1944, 1945*a*, 1945*b*). In all cases the same transverse electrical polarity could be demonstrated. CHOLODNY (1926, 1927) had already suggested that the transverse movement of growth substances would be the result of an e.m.f., and WENT (1932) formulated "Eine botanische Polaritätstheorie" (a theory of polarity in plants) after investigating the penetration of basic and acidic dyes into stem sections of *Impatiens*. According to this theory the lateral movement of growth substances would be due to a cataphoretic transport: the negatively charged anion of the growth-substance molecule would be transported to the positively charged lower side of the horizontally placed organ, resulting in an increase in the growth substance concentration in the lower side. As yet, no direct evidence has been brought forward to prove that growth substances are displaced inside the plant by electric potentials, and the question still remains whether the potential differences shown to exist in a horizontally placed plant organ are the primary effect, and, if so, whether they are adequate to displace growth substances and thus produce a geotropic curvature. In this connection SCHRANK (1945*a*) stated that "the fact that the transverse electrical polarity is established prior to the unequal distribution (of growth substances) does not necessarily mean that it is the orienting force or polarity which is essential for lateral hormone transport. It means only that the transverse electrical polarity fulfills the prime requirement of being established in the correct sequence."

Although the insight into the problem of "geotropism-growth substance" is still far from complete, the expectation seems justified that by more detailed studies of the geotropic reaction at precise dosages of growth substance, a better understanding of the relation between reacting organ and growth substance will be obtained.

From what already has been stated it can be concluded with certainty that the relation between growth substance and tissue in the upper side of a horizontally placed organ is different from that in the lower side, because—as in the case of the coleoptile of *Avena*—the lower side grows more rapidly than the upper side. This does not necessarily have to imply that more growth substance is available at the lower side. The results of Dolk and others indeed seem to indicate this possibility, but the validity of their conclusions is limited by the possibility, that in the case of equal distribution of growth substance between the upper and lower half of the coleoptile, growth substance diffuses more easily from the lower half of the coleoptile, in other words, is more mobile than the growth substance in the upper half. As professor Koningsberger, in whose laboratory this investigation was carried out, remarked during preliminary discussions concerning this subject, it cannot be excluded that a physiological difference is induced between the upper and lower side when the organ is placed horizontally, so that in this position their relation to growth substance would be different. It is not unconceivable that a difference in sensitivity to growth substance could arise, or that the reactivity to equally distributed growth substance would be increased or decreased. Fig. 1 gives a clear picture of these two factors and it also indicates the possibility of discriminating between them. The relationship is different: an increase in the sensitivity is accompanied by a lower optimal concentration, a higher reactivity yields a stronger reaction at the same optimum concentration. In practice, however, an overlapping of the two curves will often frustrate the attempt to discriminate between the two theoretical possibilities.

It is also possible that, due to a shift in the potential, more growth substance would migrate from the lipophylic phase of the protoplasm to the hydrophylic phase, so that, as in the case of the experiments of Dolk, more growth substance would be obtained in the hydrophylic block of agar at the lower side.

The method of ANKER (1954, 1956), which consists of studying growth and geotropism with coleoptiles separated from the seed and submerged in solutions, has the advantage that growth substance can be supplied at will from an external medium, within a wide range of conditions and positions of the experimental objects, so that *quantitative* studies can be carried out. The principle of this technique was therefore adopted.

The present investigation was primarily undertaken to gain more insight into the geotropic reactions of the *Avena* coleoptile, but in a certain sense the geotropic reaction was also used as an aid to study diverse growth-substance effects on the coleoptile tissue. The most interesting questions investigated were: 1). How does a coleoptile previously kept horizontally in water react if it is subsequently kept vertically in growth substance? Does some "preparatory reaction" ("Stimmungsänderung") take place which later on can be released ("ausgelöst") by growth substance, or, in other words, does a geo-induction occur in the absence of growth substance? 2). Is a back curvature after a counter-induction in the other direction possible by means of growth substance already present in the coleoptile, or is it impossible that growth-substance molecules which have already partaken in a growth-reaction, are mobilized in order to promote growth at another site in the tissue, in this case at the other side of the coleoptile? 3). Must an induced curvature first be completed before the curvature in the opposite direction, caused by rotation through 180° (the upper side becoming the lower side) begins to develop or does the latter start immediately, and 4). What is the relation between the rate at which the original curvature proceeds and that of the back curvature?

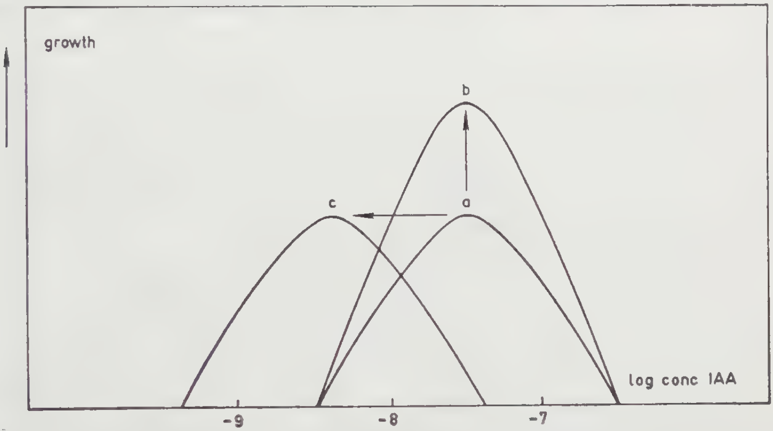

Fig. 1. Arbitrary optimum curves, showing the changes in reactivity and sensitivity of a tissue to growth substance. a → b: increased reactivity; a → c: increased sensitivity.

The results of this investigation, although mainly obtained by means of a study of the geotropic reaction, moreover yielded a contribution to the knowledge with regard to the regeneration of a physiological tip, and to the uptake, the transport and the fixation of growth substance in the coleoptile of *Avena*.

CHAPTER II

MATERIAL AND METHODS

Unhusked seeds of *Avena sativa* (var. "Siegeshafer", 1954 harvest) were placed in water in a suction flask and evacuated on the water tap for approximately 10 minutes. After they had been washed a few times, they were left to soak in tap water for two hours. The soak water was discarded and the seeds were sown in moist, sterilized vermiculite in flats and put to germinate in a ventilated darkroom which was kept at a temperature of 23° C and at a relative humidity of about 90 %. When the seedlings were just appearing above the surface of the vermiculite, 72 hours after soaking, they were exposed to orange light for 24 hours in order to suppress mesocotyl growth. Throughout the investigation, which was carried out in the above-mentioned darkroom, the only light used was from incandescent lamps, filtered by Scott OG 2 filters, so that no phototropic responses could occur.

The geotropic reaction was studied with coleoptiles which had reached a height of 2–3 cm. Such coleoptiles are physiologically still young, and show very active growth. Only straight coleoptiles of the same length were used. The coleoptile was severed from the mesocotyl, and after the primary leaf had been extracted through the opening at the base of the coleoptile, it was placed in a Van der Weij (1932) microtome (guillotine). By means of this instrument, the hollow coleoptile cylinders were simultaneously cut to a uniform length of 16–17 mm, measured from the tip of the coleoptile. In the case of decapitation, however, this manipulation was preceded by the removal of exactly 1 mm of the tip of the coleoptile; the same instrument was used.

The coleoptiles were then mounted on an apparatus similar to that described by Anker (1954). By means of such an apparatus 12 coleoptiles could simultaneously be brought from the vertical into the horizontal position and, after being brought back to the vertical position, they could automatically be turned 90° round the vertical axis, in order that shadowgraphs could be made of the curvatures. A few minor modifications, however, were made: 1) The pins onto which the coleoptiles were slipped, were slightly conical-shaped, so that coleoptiles of varying diameter could easily be mounted on the apparatus; 2) the base onto which the pins were fixed, was altered in such a way, that the coleoptiles could be rotated through 180°, so that the former upper side became the lower side. Two such apparatuses were used: one for the experimental series and the other for the control series. The two series of experiments were always carried out at the same time, because even in the course of a single day the results may vary considerably (cf. Anker, 1954). When the coleoptiles were mounted on the apparatus, care was taken that they were placed in such a way that the curvatures would develop in the plane of the two vascular bundles. According to Anker (1954), the geotropic curvatures in this plane are more uniform and more easily measurable than the curvatures in the plane of symmetry.

In the greater part of the experiments the geotropic curvature of decapitated coleoptiles took place in an aqueous solution of indole-3-acetic acid (IAA) containing 0.1 mg/l. This concentration was chosen because it is optimal for the geotropic curvature of decapitated coleoptiles (cf. Anker, 1954). The curvature of non-decapitated coleoptiles took place in water, except where otherwise stated. The fluid (one liter), either a solution of IAA or water, was contained in a cuvette made from transparent perspex, which could be raised on a platform to such a height that the coleoptiles were 1.8 cm below the surface of the solution when they were placed horizontally. In those cases that the coleoptiles were kept vertically in the solution, the platform was raised to such a height that the tips of the coleoptiles were just below the surface.

Although no experiments were undertaken on the necessity of aerating the solutions, purified air was led through, with the additional benefit of keeping the solution in constant circulation.

All shadowgraphs were made on Gevaert Document Rapid photographic paper because of its sensitivity to the phototropically inactive light used in the darkroom. A series of shadowgraphs could thus be made of the same coleoptiles. Because coleoptiles are rarely perfectly straight, shadowgraphs were also made before each experiment, so that the actual curvatures could be measured. The photographic paper was held in a plate holder by means of a glass negative on which millimeter squares had been photographed. The fact that the coleoptiles were photographed together with the squares greatly facilitated the estimation of the curvatures. The plate holder was at a distance of 1 cm behind the coleoptiles and the lamp used for exposing was at a distance of 80 cm from the plate holder. The shadowgraphs thus obtained were of good contrast and the curvatures could be measured to a high degree of accuracy by means of a protractor.

In general, the variability in biological material is rather considerable. Therefore each experiment was repeated from three to six times and the mean values calculated. The variation is expressed as the standard error of the mean, calculated by means of the formula

$$SE_m = \pm \sqrt{\frac{\Sigma\,(v-m)^2}{n\,(n-1)}} \quad \text{where}$$

n = the number of coleoptiles
$\Sigma\,(v-m)^2$ = the sum of the squared deviations from the mean.

CHAPTER III

TIME RELATION BETWEEN UPTAKE OF GROWTH SUBSTANCE AND GEOTROPIC CURVATURE

A. The uptake of growth substance in the horizontal position

When coleoptiles, that have been separated from the seed and decapitated, are kept horizontally in water, there is at first either no curvature at all or a very slight one only, the magnitude of the curvature depending on the small amount of growth substance present in the coleoptiles after decapitation. However, 120 to 150 minutes after decapitation, the regeneration of the physiological tip is completed and then the rate of curving begins to increase. Soon afterwards it reaches a constant value. This is shown in Fig. 2. In solutions of growth substances of appropriate concentration, on the other hand, decapitated coleoptiles show a well-marked curvature after 75 minutes which may practically equal that of non-decapitated coleoptiles in water. An experimental period of this short duration has the advantage that the experiment is completed before an appreciable regeneration of the physiological tip, which otherwise might obscure the results, has been effected. It is therefore clear that the geotropic curvature is dependent upon the presence of growth substance. The increase of the curvature depends on the amount of growth substance available, and its rate of development may therefore be used as a measure of the uptake of the growth substance and its utilization, a utilization, of course, depending upon the uptake of the growth substance.

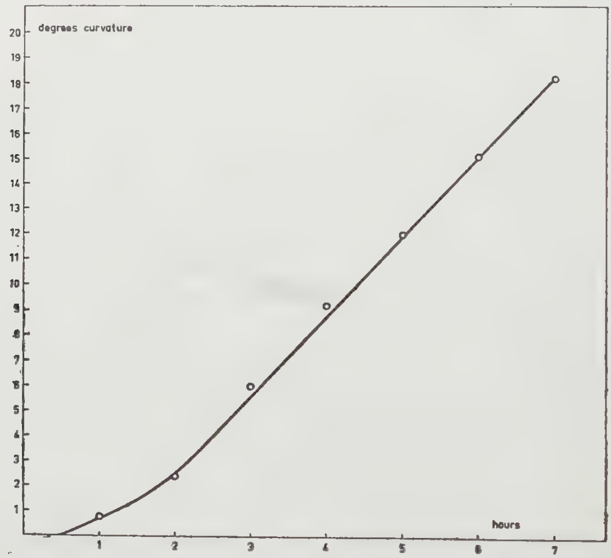

Fig. 2. Curvature of decapitated coleoptiles kept in a horizontal position in water for 7 hours.

When supplying growth substance from an external medium to decapitated coleoptiles, one meets the question whether it is possible for the coleoptiles to give a full geotropic response if they are provided with growth substance for only part of the time that they are exposed to a unilateral action of gravity. In other words, can a flood (store) of growth substance be utilized in a subsequent geotropic reaction, or do the uptake of growth substance and the curvature only proceed simultaneously?

This question was investigated in the following series of experiments. (a) During an experimental period of 75 minutes, decapitated coleoptiles were kept horizontally. During this period they were kept for either 0, 15, 30, 45 or 60 minutes in a solution of growth substance (0.1 mg IAA/l) and for the rest of the time in water. Decapitated coleoptiles that were kept for 75 minutes in the growth substance solution served as controls. The coleoptiles used in the experimental series were kept in the growth-substance solution (i) from the start of the experiment, (ii) during the latter part of the experiment or (iii) in such a way that they were brought once more in water for the last 15 minutes of the experiment, as described below and shown in Fig. 3 in which the results obtained are shown.

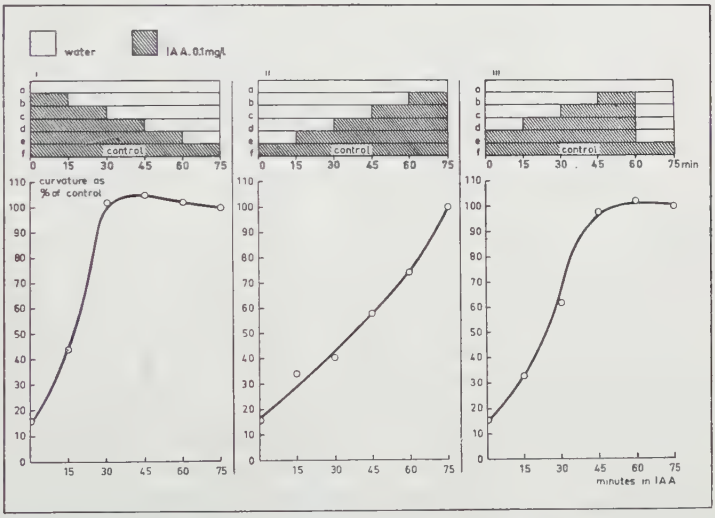

Fig. 3. Curvature of decapitated coleoptiles kept during part of the 75 minutes period of geotropic exposure in a growth-substance solution (0.1 mg IAA/l). Magnitude of the curvature expressed as a percentage of the curvature of the controls which were kept in the growth-substance solution for the entire experimental period. (Average curvature of the controls: 10° = 100 %).

All coleoptiles kept horizontally for 75 minutes:

(i) (a) 75 minutes in water
(b) 15 minutes in growth-substance solution, 60 minutes in water.
(c) 30 ,, ,, ,, ,, ,, 45 ,, ,, ,,
(d) 45 ,, ,, ,, ,, ,, 30 ,, ,, ,,
(e) 60 ,, ,, ,, ,, ,, 15 ,, ,, ,,
(f) 75 ,, ,, ,, ,, ,, (controls).

(ii) (a) 75 minutes in water
(b) 60 minutes in water, 15 minutes in growth-substance solution.
(c) 45 ,, ,, ,, 30 ,, ,, ,, ,, ,,
(d) 30 ,, ,, ,, 45 ,, ,, ,, ,, ,,
(e) 15 ,, ,, ,, 60 ,, ,, ,, ,, ,,
(f) 75 minutes in growth-substance solution (controls).

(iii) (a) 75 minutes in water
(b) 45 minutes in water, 15 minutes in growth-substance soln., 15 min. water
(c) 30 ,, ,, ,, 30 ,, ,, ,, ,, ,, 15 ,, ,,
(d) 15 ,, ,, ,, 45 ,, ,, ,, ,, ,, 15 ,, ,,
(e) 0 ,, ,, ,, 60 ,, ,, ,, ,, ,, 15 ,, ,,
(f) 75 minutes in growth-substance solution (controls)

From the results obtained in series (i) it can be seen that the amount of growth substance taken up during 15 minutes (one-fifth of the experimental period) is already sufficient to ensure a curvature of about 44 % of the control. In subsequent experiments (e.g. Fig. 4, p. 13) it was found that curvatures which could be measured by the method employed, only became apparent 20 to 30 minutes after the coleoptiles had been placed horizontally. SCHRANK (1945*a*), by whom the moment the upward curvature starts, was determined by means of microscopic observation, found that in the case of intact coleoptiles this is 22 minutes after the coleoptiles had been placed in a horizontal position. During the 15 minutes that the coleoptiles were kept in the growth-substance solution, there is no measurable curvature. The values registered in (i)*b* therefore evidently pertain to curvatures developing after the coleoptiles have been removed from the growth-substance solution to water. The development of the curvature accordingly is made possible by the growth substance absorbed during the 15 minutes the coleoptiles stayed in the growth-substance solution and does not require a continuous supply of growth substance from the medium. For the moment it remains uncertain whether the growth substance is taken up in different amounts by the upper and lower halves of the horizontally placed coleoptile, or whether changes in the growth substance pattern take place later on.

The results from (i) further show that a period of 30 minutes in the horizontal position in the growth-substance solution is sufficient for the development of a curvature equalling that of the controls, which had been kept in the growth-substance solution for the whole period of 75 minutes. There is no indication that the rate of the development of the curvature is more rapid in the beginning, i.e. during the latter part of the first 30 minutes, than afterwards. It will be shown later that the rate of increase of the curvature remains constant over a period of several hours. One may safely assume that the rate of development of the curvature is the same in both experimental and control coleoptiles throughout the experimental period. This was confirmed by the experiments described in a following section (p. 13). If the geotropic curvature is dependent upon the immediate availability of growth substance, which is likely since the geotropic curvature is a growth phenomenon, one must assume that by an excessive growth-substance uptake during the period of 30 minutes, the further development of the curvature is ensured for another 45 minutes. Even if some of the growth substance should be lost by diffusion into the surrounding water, a sufficient amount, at any rate, remains available to ensure the further development of the geotropic curvature during the period the experiment lasts.

The results of series (ii) and (iii) agree very well with each other: in both sets of experiments there is an increase in the magnitude of the curvature with an increase in the time the coleoptiles are kept in the growth-substance solution. During the time that the coleoptiles are kept in water the curvature remains negligible; in fact, the development of the curvature only starts after the coleoptiles have been placed in the growth-substance solution. In the following instances the period elapsing between the moment of introducing the growth substance and the end of the experiment will be designated as "conditioning time". In experiment *c* of series (ii) and in experiment *b* of series (iii) the conditioning time is 30 minutes and the curvature is 36 % and 35 % respectively of that of the controls. With a conditioning time of 45 minutes (experiment *d* of series (ii) and experiment *c* of series (iii)), the curvatures are 56 % and 62 % respectively, of the controls, which is to be regarded as a sufficient agreement. In all cases observed it is seen that a transfer of the coleoptiles from the growth-substance solution to water (series (iii)), does not affect the magnitude of the subsequent curvature, at least if the experiment is continued for a limited period only. The results of experiment *e* of series (ii), however, do not agree with those of experiment *d* of series (iii). In experiment *e* of series (ii) the curvature is 74 % of that of the controls while in experiment *d* of series (iii) the curvature equals that of the controls. In both cases the conditioning time is the same, viz. 60 minutes, and as it was shown in the two pairs of experiments described previously that a period of 15 minutes in water following the immersion in the growth-substance solution does not affect the final magnitude of the curvature, the difference in degree of curvature cannot be understood unless one assumes that the values obtained in experiment *d* of series (iii) are incidentally too high. As will be seen later, there is, after a lag time ("latency time") of 20 to 30 minutes a linear proportionality between the magnitude of the curvature and the conditioning time when the coleoptiles are kept horizontally in the growth-substance solution (p. 14). A conditioning time of 60 minutes therefore should yield a smaller curvature than one of 75 minutes.

(b) The fact has already been mentioned that during an immersion of only 15 minutes in the growth-substance solution enough growth substance is taken up to ensure at the end of the 75 minutes a curvature far in excess of that shown by decapitated coleoptiles kept horizontally in *water* for 75 minutes.

An exact estimation of the rate of growth-substance uptake from the observed curvatures, however, is impossible since the uptake proceeds more rapidly than the utilization. If this leads to an accumulation of growth substance in the coleoptile, so that the inner concentration becomes higher than that of the solution, it becomes possible that part of it is lost again by diffusion. If the coleoptiles are transferred to water, as was done in the present experiments, even without accumulation some auxin may be lost in this way. The probability of growth-substance loss is very small when the submersion time is short, since the length of the section is relatively great and a diffusion through the cuticle is not to be expected at the concentration used.

To investigate the influence of an immersion in a growth-substance solution, shorter than 15 minutes, decapitated coleoptiles were kept in a growth-substance solution (0.1 mg IAA/l) for 5 and for 10 minutes and then in water for 70 and 65 minutes respectively. In these series of experiments, the controls were decapitated coleoptiles kept horizontally in *water* for 75 minutes, in contrast to the previous series of experiments, where coleoptiles kept horizontally in *growth substance* for 75 minutes served as the controls.

The results are presented in Tables *Ia* and *Ib* respectively.

TABLE Ia

Curvature of decapitated coleoptiles kept horizontally, first in a growth-substance solution (0.1 mg IAA/l) for 5 minutes and then for a further 70 minutes in water. Controls: kept horizontally in water for 75 minutes.

Curvature in degrees	
5 minutes in the growth-substance solution, 70 minutes in water	75 minutes in water (controls)
4.6	3.0
4.1	4.1
4.2	2.8
4.7	4.0
4.8	2.8
Av. 4.5 ± 0.14	3.3 ± 0.29

TABLE Ib

Curvature of decapitated coleoptiles kept horizontally, first in a growth-substance solution (0.1 mg IAA/l) for 10 minutes and than for a further 65 minutes in water. Controls: kept horizontally in water for 75 minutes.

Curvature in degrees	
10 minutes in the growth-substance solution, 65 minutes in water	75 minutes in water (controls)
4.4	2.3
5.0	2.6
5.4	3.3
4.6	2.3
Av. 4.8 ± 0.22	2.6 ± 0.24

From the results it can be seen that when the coleoptiles are kept for only 5 minutes in a growth-substance solution, the curvature is 1.4 times as high as the curvature of the coleoptiles kept in water all the time. When kept for 10 minutes in the growth-substance solution, the curvature is 1.8 times as high. It is clear that the growth substance taken up during these 5 or 10 minutes is subsequently used for the development of the geotropic curvature which, however, starts only some 20 minutes later. This means that at least part of the IAA is retained during this interval and that it remains available for the development of the geotropic curvature.

The curvature of these coleoptiles was much smaller than that of coleoptiles which are kept in a growth-substance solution for 75 minutes, which is usually 10° or more. The amount of growth substance taken up in such short periods is therefore insufficient to ensure the development of a curvature of maximum magnitude.

(c) In the experiments described under (a) it was found that a period of 30 minutes in a horizontal position in a solution of growth substance is sufficient to ensure the further development of the geotropic curvature in water for at least 45 minutes and at the same rate as in the control coleoptiles which remained in the growth-substance solution. It was now investigated how long the effect which an immersion during 30 minutes in a growth-substance solution exercises on the further development of the curvature in water, really lasts. The experimental procedure is given below and the results are shown in Fig. 4.

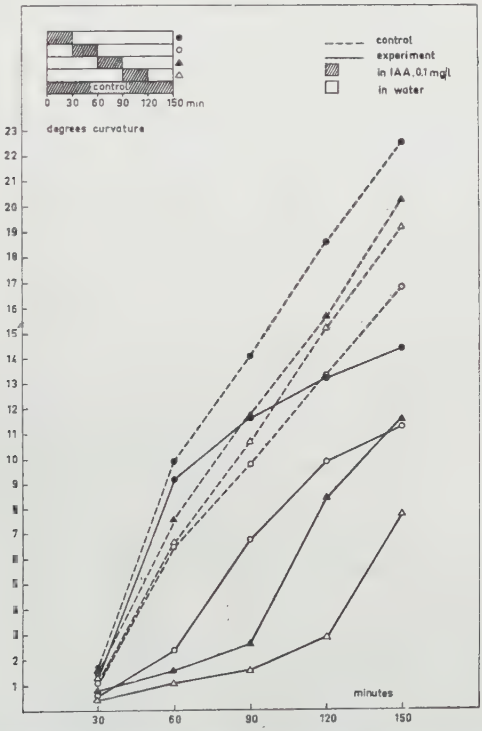

Fig. 4. Curvature of decapitated coleoptiles kept horizontally in water before and after a period of 30 minutes in a growth-substance solution (0.1 mg IAA/l). Controls: decapitated coleoptiles kept horizontally in the growth-substance solution for the whole of the experimental period.

Decapitated coleoptiles were kept horizontally for 150 minutes: in total they were kept in water for 120 minutes and for the remaining 30 minutes in a growth-substance solution (0.1 mg IAA/l). The distribution of the periods in the growth-substance solution varied in the different series of experiments. The controls were kept horizontally in a solution of growth substance for the entire experimental period of 150 minutes. The time-table for the different series is as follows:

(a) 30 minutes in the growth-substance solution, 120 minutes in water.
(b) 30 minutes in water, 30 minutes in g.s., 90 minutes in water.
(c) 60 ,, ,, ,, 30 ,, ,, ,, 60 ,, ,, ,,
(d) 90 ,, ,, ,, 30 ,, ,, ,, 30 ,, ,, ,,
(e) 150 minutes in the growth-substance solution (controls).

This procedure also enabled one to study the possible influence of a period passed horizontally in water, preceding that in which the growth substance was added, on the rate of curving. In this way data could be obtained with regard to an eventual occurrence of introductory, although not outwardly visible, processes induced by the gravitational force in the absence of growth substance.

In the control series the curvature remained small during the first 30 minutes. This period was followed by one of rapid increase in the rate of curvature, and the value now reached remained more or less constant up to the end of the experiment. In the experimental series the curvature increased but very little during the period preceding the addition of growth substance. A slight increase in the curving rate was noticeable during the 30 minutes of immersion in the IAA solution. During the next 30 minutes, i.e. after the coleoptiles had been brought back into water, there was a rapid increase in the curvature, followed by a decrease lasting until the end of the experiment. When the coleoptiles were kept in the growth-substance solution at the start of the experiment or during the second period of 30 minutes, a marked decrease in the rate of curving was noticeable in the final period of the experiment.

The amount of growth substance taken up from the solution apparently is sufficient to ensure the maintenance of the curving rate at a more or less constant level for at least 45 minutes after the transfer of the coleoptiles into water. Then the inner growth-substance concentration becomes the limiting factor.

If in the experimental series the value of the curvature at the moment the coleoptiles are immersed in the growth-substance solution is subtracted from the one reached 60 minutes later, a value is obtained that is nearly the same as that found in the control series 60 minutes after the beginning of the experiment. The method of calculation is shown below:

(a) IAA added at time zero:
Curvature at 0 minutes . . . .: 0.0°
,, after 60 minutes . . . .: 9.2°
,, of controls after 60 minutes . . . .: 9.9°
Difference: 0.7°

(b) IAA added after 30 minutes:
Curvature at that moment: 0.6°
„ 60 minutes later: 6.8°
Increase of curvature during these 60 minutes: 6.2°
Curvature of controls after 60 minutes: 6.5°
Difference: 0.3°

(c) IAA added after 60 minutes:
Curvature at that moment: 1.6°
„ 60 minutes later: 8.5°
Increase of curvature during these 60 minutes: 6.9°
Curvature of controls after 60 minutes: 7.6°
Difference: 0.7°

(d) IAA added after 90 minutes:
Curvature at that moment: 1.6°
„ 60 minutes later: 7.8°
Increase of curvature during these 60 minutes: 6.2°
Curvature of controls after 60 minutes: 6.7°
Difference: 0.5°

In all cases the curvature in the experimental series, 60 minutes after submersion in the growth-substance solution, is only slightly less than that of the control series after the first 60 minutes. The length of time that the coleoptiles had been kept horizontally in water before growth substance was added, apparently did not markedly influence the subsequent curvature.

The conclusion to be drawn from these experiments is that during the time the coleoptiles are kept horizontally in water, there are no preparatory physical or chemical changes in the coleoptile which would make it either more receptive to the gravitational force, or more reactive once the growth substance is taken up. This indicates a close relation between the presence of growth substance and the "perception" of the gravitational force by the coleoptile.

B. THE UPTAKE OF GROWTH SUBSTANCE IN THE VERTICAL POSITION

(*1*) *Decapitated coleoptiles*

In the previous section (A) it has been demonstrated that decapitated coleoptiles kept horizontally in a 0.1 mg/l IAA-solution for only a short time, take up enough growth substance to ensure a prolonged development of the geotropic curvature when transferred to water.

It was now investigated what geotropic curvatures decapitated coleoptiles exhibit in water, when the growth substance was taken up in a vertical position.

(a) Decapitated coleoptiles were kept vertically in a solution containing 0.1 mg IAA/l for periods ranging from 5 to 90 minutes and then horizontally in water for a further 75 minutes The experiments therefore were completed before an appreciable regeneration of the physiological tip could have been effected. It is known from the work of GORTER (1927) and confirmed by the present results (p. 40) that no regeneration of the physiological tip occurs when the decapitated coleoptiles are supplied with IAA. According to TSI-TUNG LI (1930) the process is completed 120 to 150 minutes after 1 mm of the tip of a coleoptile still attached to the seed, is removed.

In the control series decapitated coleoptiles were kept vertically in water for the same length of time as the coleoptiles of the experimental series were kept vertically in the growth-substance solution, and then for 75 minutes horizontally in the growth-substance solution. The curvatures were measured after the coleoptiles had been in the horizontal position for 75 minutes; the results are shown in Table II.

TABLE II

Curvature of decapitated coleoptiles, first kept vertically in a growth-substance solution (0.1 mg IAA/l) for various lengths of time and then horizontally in water for 75 minutes. Controls: decapitated coleoptiles first kept vertically in water for the same period as the experimental coleoptiles were kept vertically in the growth-substance solution, and then horizontally in a growth-substance solution (0.1 mg IAA/l) for 75 minutes. Curvatures in experimental and control series measured after the same length of time.

Minutes in vertical position	Curvature in degrees		Curvature expt. as % of the controls
	Experimental coleoptiles	Control coleoptiles	
0	1.5 ± 0.19	8.7 ± 0.84	17
5	5.1 ± 1.27	12.0 ± 1.76	43
10	5.1 ± 0.82	13.6 ± 0.72	38
20	5.9 ± 0.44	13.8 ± 0.44	43
25	3.6 ± 0.07	10.9 ± 0.20	33
30	3.9 ± 0.22	14.8 ± 0.33	26
40	5.3 ± 0.75	13.9 ± 1.30	38
60	5.3 ± 0.54	14.2 ± 1.82	37
90	6.7 ± 0.83	15.6 ± 0.52	43

From the results presented in Table II it is clear that there is not much difference in the curvature of the coleoptiles, whether they were kept in the growth-substance solution for only 5 minutes or for 90 minutes. Although there is some variation in the absolute value of the curvatures, they all fluctuate between 26 % and 43 % of the value reached by the curvature of the controls. In all instances the curvature is larger than that of coleoptiles which were placed horizontally in water but were not previously kept vertically in a growth-substance solution, for in that case the curvature measured only 1.5° ± 0.19.

Although the growth substance was provided in a concentration sub-optimal for growth (ANKER, 1956), the results indicate that the amount taken up in the vertical position is not entirely consumed in the ordinary growth process, but that part of it remains available for a subsequent geotropic reaction. Whether the coleoptiles remain from 5 to 90 minutes vertically in the growth-substance solution, this part proves to be independent of the time during which the growth substance is taken up. This would indicate that the uptake of growth substance proceeds more rapidly than its fixation to, or utilization by the protoplasm. Since both processes are proceeding at a constant rate, a steady state is soon reached, in which a certain amount of growth substance ("free auxin") remains available in the cells. In the previous section (p. 10) there were indications for the assumption that the growth substance, once it has been taken up by the coleoptile, is stored in such a way that it cannot be lost into the surrounding water. It therefore does not seem likely that the growth substance taken up in the vertical position is lost into the water when the coleoptiles are placed horizontally, and that the small size of the curvature would be due to this cause.

(b) From the preceding series of experiments it is clear that in any case part of the growth substance taken up in the vertical position can be used in the development of a geotropic curvature when the coleoptiles are placed horizontally in water.

Next, the possibility was investigated of a summation of the effects due to the amount of growth substance taken up first during a stay in the vertical position and then in a horizontal one in the same solution. In view of the results obtained by ANKER (1954, 1956), a summation would result in a small decrease in the magnitude of the curvature, since the concentration of 0.1 mg IAA/l in the medium was already nearly supra-optimal.

Decapitated coleoptiles were kept vertically in a growth-substance solution (0.1 mg IAA/l) for different lengths of time and then horizontally in the same solution for a further 75 minutes. In the control series the coleoptiles were kept vertically in water for the same length of time as the experimental ones were kept vertically in the growth-substance solution, and then they were kept horizontally in the growth-substance solution for 75 minutes. The results are given in Table III.

TABLE III

Curvature of decapitated coleoptiles first kept vertically in a growth-substance solution (0.1 mg IAA/l) for various lengths of time and then horizontally for a further 75 minutes, also in the growth-substance solution. Controls: decapitated coleoptiles first kept vertically in water for the same period as the experimental coleoptiles were kept vertically in the growth-substance solution, and then horizontally in the growth-substance solution for 75 minutes.

Minutes in vertical position	Curvature in degrees		Curvature expt. as % of controls
	Experimental coleoptiles	Control coleoptiles	
10	10.7 ± 0.91	11.2 ± 1.94	96
20	11.9 ± 0.84	12.7 ± 1.22	94
40	11.2 ± 1.12	11.7 ± 1.07	96
80	13.6 ± 1.58	12.4 ± 0.26	110

The curvature of the experimental series is slightly smaller than that of the control ones. If the differences between the curvature of the control and the experimental series were significant, this could easily be explained by the observations of Anker just-mentioned. These results agree well with the explanation (p. 10) that a constant ratio between the uptake and utilization of the growth substance is soon reached, so that a certain amount of free growth substance remains available in the cells.

(c) Anker (1956) has shown that no geotropic curvatures occur in IAA solutions of concentrations that are optimal for straight growth (0.6 mg IAA/l) or higher. It seemed worthwhile to investigate the effect exercised by a high growth-substance concentration applied before the coleoptiles were placed horizontally, on the magnitude of the geotropic reaction, when the latter is carried out in a solution of optimal IAA concentration. Therefore experiments were carried out in which the coleoptiles were kept vertically for periods of 10, 20, 40, and 80 minutes in a solution containing 1.0 mg IAA/l and then horizontally for a further 75 minutes in a solution containing 0.1 mg IAA/l. In this case the controls were kept vertically in water for the same length of time as the coleoptiles of the experimental series were kept vertically in the growth-substance solution and then horizontally in a growth-substance solution (0.1 mg IAA/l) for 75 minutes. The results are shown in Table IV and in Fig. 5.

TABLE IV

Curvature of decapitated coleoptiles first kept vertically in a growth-substance solution (1.0 mg IAA/l) for various lengths of time and then horizontally in a growth-substance solution (0.1 mg IAA/l) for 75 minutes. Controls: decapitated coleoptiles kept vertically in water for the same period as the experimental coleoptiles were kept vertically in the growth-substance solution, and then horizontally in a growth-substance solution (0.1 mg IAA/l) for 75 minutes.

Minutes in vertical position	Curvature in degrees		Curvature in experimental series as % of those of controls
	Experimental coleoptiles	Control coleoptiles	
10	7.6 ± 0.51	10.6 ± 0.76	72
20	6.1 ± 0.31	9.9 ± 0.75	62
40	5.5 ± 0.40	10.3 ± 0.65	53
80	4.9 ± 0.45	12.7 ± 0.96	39

It is clear that a "flooding" of the coleoptile with growth substance, prior to a geotropic exposure, has a strongly decreasing effect on the magnitude of the curvature. Even such a short period as 10 minutes has a marked depressing effect on the ultimate magnitude of the curvature, again indicating that the uptake of growth substance by decapitated coleoptiles is a rapid process.

There is no reason to suppose that the growth-substance concentration was supra-optimal for straight growth. The geotropic curvature already decreases considerably at concentrations which are far below the saturation value for straight growth. The relation between the optimal concentrations for straight growth and for geotropism is dealt with by Anker (1956). Maximal geotropic curvature occurred in that limited range of concentrations where small differences in the concentration cause large differences in straight growth. The interpretation of the present decrease in curvature is obvious on account of the results of Anker (1956). Here also the concentration inside the coleoptiles was supra-optimal for the geotropic curvature and about optimal for straight growth.

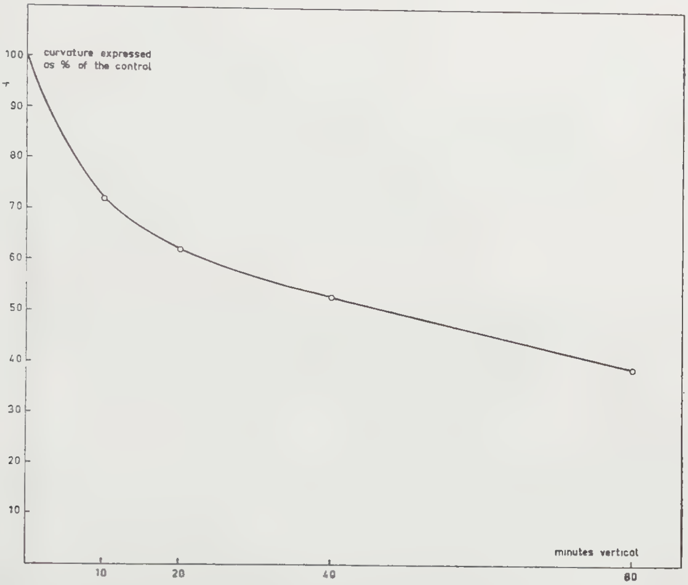

Fig. 5. Curvature of decapitated coleoptiles first kept vertically in a solution containing 1.0 mg IAA/l and then horizontally in a solution containing 0.1 mg IAA/l for 75 minutes; curvature expressed as a percentage of that of the controls. Controls: coleoptiles first kept vertically in water and then horizontally in the growth-substance (0.1 mg IAA/l) for 75 minutes.

(2) *Non-decapitated coleoptiles*

The same kind of experiments was performed with non-decapitated coleoptiles. The growth substance was added in various concentrations, in some experiments while the coleoptiles were kept vertically and in others while they were kept horizontally. The growth substance now did not enter the coleoptile via a cut surface, as in the experiments with decapitated coleoptiles, but could only enter through the cuticle. In the previous experiments the latter way of entrance, of course, also occurs; however, it was shown by Anker (1954) that at the low concentration of 0.1 mg IAA/l the curvatures of non-decapitated coleoptiles are equal to those, shown by non-decapitated coleoptiles kept in water. This means that with this concentration the amount of IAA passing through the cuticle in the experimental period of 75 minutes is negligible. There is no possibility of a supply of growth substance via the basal cut surface since it is a well-established fact that auxin transport in the *Avena* coleoptile is strictly polar, from tip to base only.

Another difference with the former experiments in which decapitated coleoptiles were used, is that the effect of growth substance absorbed from outside is now superimposed on the action of natural auxin produced in the tip. A complication will occur if the growth substance supplied from outside enters into the tip and then interferes with the auxin production.

For the above-mentioned reason, viz. that during the relatively short period of 75 minutes there is no appreciable (in any case no observable) effect of the entrance of growth substance through the cuticle, in the present experiments higher concentrations of IAA were used, viz. 0.2 mg/l, 0.5 mg/l, 0.6 mg/l and 1.0 mg/l. The coleoptiles were kept horizontally in the solutions for 75 minutes, and the curvatures were compared with those of non-decapitated coleoptiles kept horizontally in water for the same period. The results are shown in Table V.

Table v

Curvature of non-decapitated coleoptiles kept horizontally for 75 minutes in growth-substance solutions of different concentrations. Controls: non-decapitated coleoptiles kept horizontally for 75 minutes in water.

Concentration of IAA in mg/l in the experimental series	Curvature in degrees		Curvature expt. as % of the controls
	Experimental coleoptiles in growth-substance solution	Control coleoptiles in water	
0.2	20.2 ± 1.21	20.5 ± 1.56	99
0.5	16.8 ± 0.98	14.8 ± 0.77	114
0.6	14.6 ± 1.11	12.3 ± 0.89	119
1.0	15.2 ± 1.32	17.6 ± 1.07	86

From the table it is clear that even in a solution of 0.2 mg/l the curvature carried out under the influence of the natural auxin is not affected by the IAA absorbed from outside. In the higher concentrations of IAA, namely of 0.5 and of 0.6 mg/l, on the other hand, the curvatures were larger than those of the controls. In the highest concentration used, 1.0 mg/l, the curvature showed a slight decrease and in some coleoptiles even positive curvatures were recorded. These results support the estimation of Anker (1956) that the inner auxin concentration in coleoptiles is very near to the optimal one for the geotropic response.

In another series of experiments non-decapitated coleoptiles were first kept vertically in solutions of different IAA concentrations for various lengths of time and then horizontally in water for a further 75 minutes. In the control series, non-decapitated coleoptiles were kept vertically in water for the same length of time that the coleoptiles of the experimental series were kept vertically in the growth-substance solution, and then horizontally for 75 minutes in water. The results are given in Tables VI, VII and VIII.

These results are different from those recorded in Table V. In the latter instance decreases as well as increases of the curvature were observed, depending on the IAA-concentration of the outer solution. In the present experiments the curvatures of the experimental coleoptiles are all smaller than those of the controls. The difference may find its explanation in the experimental procedure. The fact that the curvatures arose during or after the supply of growth substance could have been of paramount importance.

Table VI

Concentration of growth-substance solution 0.1 mg IAA/l. Non-decapitated coleoptiles first kept vertically in the growth-substance solution for various lengths of time and then horizontally in water for 75 minutes. Controls: non-decapitated coleoptiles kept vertically and horizontally in water for the same lengths of time as the experimental coleoptiles.

Minutes in vertical position	Curvature in degrees		Curvature in experimental series as % of those of controls
	Experimental coleoptiles	Control coleoptiles	
10	18.2 ± 0.48	20.5 ± 0.56	89
20	18.0 ± 1.21	20.2 ± 1.03	89
40	16.3 ± 0.85	18.9 ± 1.75	86
80	15.8 ± 0.65	17.7 ± 0.61	89

Table VII

Concentration of growth-substance solution 0.5 mg IAA/l. Non-decapitated coleoptiles first kept vertically in the growth-substance solution for various lengths of time and then horizontally in water for 75 minutes. Controls: non-decapitated coleoptiles kept vertically and horizontally in water for the same lengths of time as the experimental coleoptiles.

Minutes in vertical position	Curvature in degrees		Curvature in experimental series as % of those of controls
	Experimental coleoptiles	Control coleoptiles	
10	14.7 ± 0.79	16.1 ± 0.70	91
20	13.1 ± 0.50	14.8 ± 0.46	89
40	12.5 ± 0.44	14.9 ± 0.52	84
80	11.6 ± 0.42	14.8 ± 0.28	78

Table VIII

Concentration of growth-substance solution 0.6 mg IAA/l. Non-decapitated coleoptiles first kept vertically in the growth-substance solution for various lengths of time and then horizontally in water for 75 minutes. Controls: non-decapitated coleoptiles kept vertically and horizontally in water for the same lengths of time as the experimental coleoptiles.

Minutes in vertical position	Curvature in degrees		Curvature in experimental series as % of those of controls
	Experimental coleoptiles	Control coleoptiles	
10	13.9 ± 0.85	16.1 ± 0.43	86
20	13.9 ± 0.49	14.2 ± 0.56	98
40	10.2 ± 0.53	13.3 ± 0.91	77
80	10.2 ± 0.81	12.8 ± 0.91	80

It is difficult to assume that the decreases in the curvature, for example those shown in table VI, where the concentration of the growth-substance solution was only 0.1 mg/l was due to an over-dosage of IAA since the geotropic response in this solution and even in one of double the concentration (0.2 mg/l, see above) is not impaired. If there were an over-dosage of IAA one would expect the decreasing effect exercised by the outer solution on the curvature to increase with the time the coleoptiles are immersed in the solution.

A possible explanation is that the decreased curving rate is due to under-dosage of growth substance. This means that the coleoptile tip produces less auxin in a growth-substance solution than in water. A depressing effect exercised by small amounts of growth substance diffusing through the epiderm of the tip on the auxin production would be in accordance with the inhibition of the regeneration of the physiological tip by growth substance absorbed from outside.

CHAPTER IV

EFFECTS OF SHORT AND OF ANTAGONISTIC HORIZONTAL EXPOSURES

When geotropically stimulated coleoptiles are placed vertically or are rotated along the horizontal axis of a klinostat, the geotropic curvature continues to increase. After a while, however, the process is reversed and finally the coleoptiles are again more or less perfectly straight. To obtain this result, it is not necessary to continue the lateral exposition to gravity until the curvature becomes visible. Rutten-Pekelharing (1910) found that such a short exposure as 4 to 5 minutes results in a perceptible curvature.

In this chapter the results are reported of an investigation in which the above-mentioned phenomenon was studied more closely. The experiments were carried out with decapitated coleoptiles in an IAA-solution of 0.1 mg/l and with non-decapitated coleoptiles in water.

A. Curvature of coleoptiles that have been placed vertically after a geotropic exposure

Non-decapitated coleoptiles were kept horizontally in water for a certain length of time and then placed vertically, also in water. Decapitated coleoptiles were kept horizontally in a growth-substance solution (0.1 mg IAA/l) for a certain length of time and then vertically either in the same solution or in water. The length of the period of geo-induction varied from 30 to 90 minutes; the results, shown in Fig. 6, may be regarded as typical of the general behaviour of coleoptiles in this type of experiment. Whether the coleoptiles were kept horizontally for short or for long periods, the behaviour was the same; there were, of course, differences in the absolute values of the curvatures.

It appears that non-decapitated coleoptiles start curving 20 to 30 minutes after being placed horizontally. Upon being placed vertically, the geotropic curvature continues for another 30 minutes and then a straightening of the coleoptile takes place rather rapidly. The straightening proceeds from the base towards the tip until the coleoptile is once more straight. In the case of decapitated coleoptiles kept both horizontally and vertically in a growth-substance solution, exactly the same happens. Therefore, there is a striking conformity between the reactions of the non-decapitated coleoptiles and the decapitated ones kept in the IAA solution of 0.1 mg/l. In the case of decapitated coleoptiles kept horizontally in the growth-substance solution and vertically in water, however, the curvature increases during the first 30 minutes after the coleoptiles have been placed vertically in the same way as in the previous cases and then here too the curving comes to a standstill but there is no appreciable straightening of the coleoptiles.

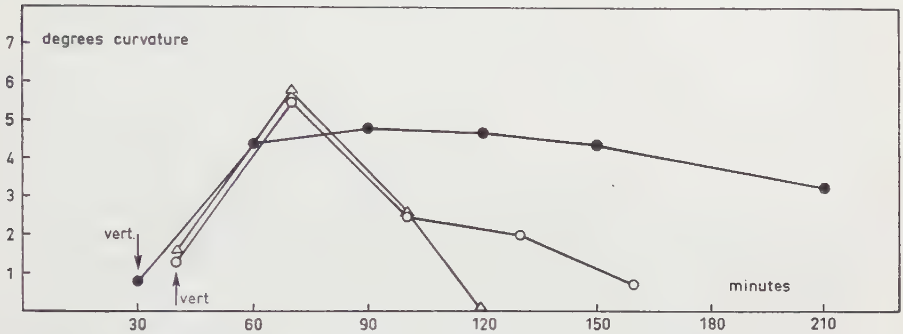

Fig. 6. Geotropic curvatures of coleoptiles carried out in the vertical position after periods of 30 or 40 minutes in the horizontal position. Triangles: non-decapitated coleoptiles, horizontal and vertical in water; circles: decapitated coleoptiles, horizontal and vertical in a growth-substance solution (0.1 mg IAA/l); dots: decapitated coleoptiles, horizontal in a growth-substance solution (0.1 mg IAA/l), vertical in water. Arrows indicate when the coleoptiles were placed vertically.

From these results one must conclude that the changes brought about in the coleoptile by an exposure to gravity disappear within 30 minutes and that in the meantime reactions are initiated to restore the original situation. In this process of restoration growth substance is evidently involved since a straightening reaction did not occur when decapitated coleoptiles were placed vertically in water.

This lack of restoration in the absence of growth substance is of a similar nature as what might be called the absence of a "preparatory or introductory process" when coleoptiles are placed horizontally in water and then vertically in a growth-substance solution. One could suppose that in a horizontal position in the absence of growth substance, the decapitated coleoptile changes internally. Such an "introductory process" could consist of a change either in the sensitivity or in the reactivity of the coleoptile. If it should occur, the coleoptile would show a curvature when placed vertically in a growth-substance solution after a horizontal exposure in water. That such an introductory process does not exist is clearly demonstrated by the following experiment in which decapitated coleoptiles were first kept horizontally in water for periods of 30 or 40 minutes, during which time no curvatures were registered, and then vertically in a growth-substance solution (0.1 mg IAA/l). No geotropic curvatures could be ascertained. This again shows that the presence of growth substance in the coleoptile is required in order that a geotropic induction may take place.

This explanation would have to be discarded if it should appear that an introductory process actually occurs in the horizontal position. In that case it would have to be assumed that it is abolished in the vertical position before the effect of the growth substance becomes apparent. In all the preceding experiments it has been found that this effect only becomes visible after 20 to 30 minutes.

The following experiments do not yield any evidence for this explanation.

B. THE CURVATURE OF COLEOPTILES DURING ANTAGONISTIC EXPOSURES TO GRAVITY

In a way the effect of antagonistic exposures to gravity on the curvature has already been illustrated by the experiments under (A). The counterinduction obtained by curved coleoptiles being placed vertically, however, is very small. To study some aspects of the resulting curvatures more quantitatively, the coleoptiles were kept horizontally for a certain length of time, first in one position and then they were rotated through 180°, so that the former upper side became the lower

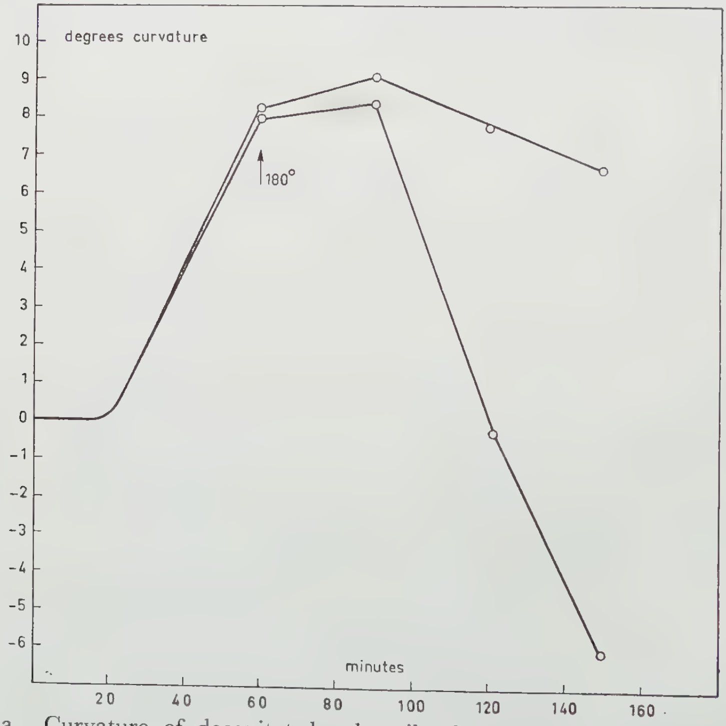

Fig. 7a. Curvature of decapitated coleoptiles kept horizontally in a growth-substance solution (0.1 mg IAA/l), first in one position for 60 minutes and then rotated through 180°. Upper line: kept in water after rotation; lower line: left in the growth-substance solution after rotation.

side. The curvature induced in the latter position would then be in a direction opposite to the initial one.

In preliminary experiments, decapitated coleoptiles were kept horizontally in a growth-substance solution (0.1 mg IAA/l) for 60 or 90 minutes and then rotated through 180°, after which they were kept either in water or remained in the growth-substance solution. The curvatures exhibited by such coleoptiles are shown in Fig. 7*a* and in Fig. 7*b*.

As usual, the coleoptiles started curving about 20 minutes after the moment they were placed horizontally. After they had been rotated through 180° they kept on curving in the initial direction for another 20 to 30 minutes. Then the coleoptiles left in the growth-substance solution began to curve rapidly in the opposite direction; it looked even as if the "back curvature" proceeded more rapidly than the initial curvature. In the case of coleoptiles kept in water after rotation through 180°, these also started curving in the opposite direction after 30 minutes. The "back curvature", however, was much slower than the original

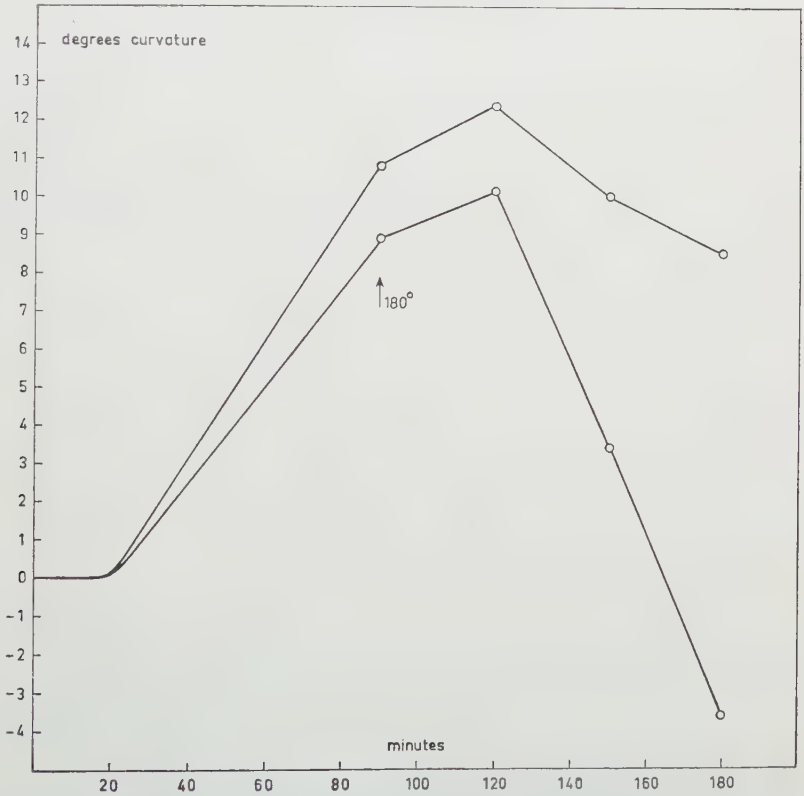

Fig. 7b. Curvature of decapitated coleoptiles kept horizontally in a growth-substance solution (0.1 mg IAA/l), first for 90 minutes in one position and then rotated through 180°. Upper line: kept in water after rotation; lower line: left in the growth-substance solution after rotation.

curvature. Here again it is observed that growth substance must be immediately available for the development of a geotropic curvature. As soon as the supply is discontinued the curving rate diminishes and, as in the present case, the effect of the antagonistic exposure is small. Complete absence of a back curvature was not found; apparently there is some auxin left to be utilized. The bulk of the growth substance, however, is bound—probably used up in the growth process during the first curvature—at any rate, it is not available for the back curvature.

The behaviour of non-decapitated coleoptiles in water (not shown in the figures) was exactly the same as that just described for decapitated coleoptiles kept in a solution of growth substance before and after rotation.

There were indications that the back curvature was more rapid than the original one, and to investigate this possibility, decapitated coleoptiles were kept horizontally in a growth-substance solution (0.1 mg IAA/l) for periods of 10, 20 and 90 minutes and then rotated through 180°, after which they were still kept in the same solution. To ensure that sufficient growth substance had been taken up for a proper geotropic reaction after 10 and 20 minutes, several experiments were also done in which the coleoptiles were pretreated with growth substance in the vertical position: they were kept vertically in the growth substance for 30 minutes before they were placed horizontally. An example is shown in fig. 11. This shows that the pretreatment had no effect. Growth substance was therefore not a limiting factor in these experiments. To compare the rates of curvature, control coleoptiles were kept horizontally in the growth-substance solution for the whole of the experimental

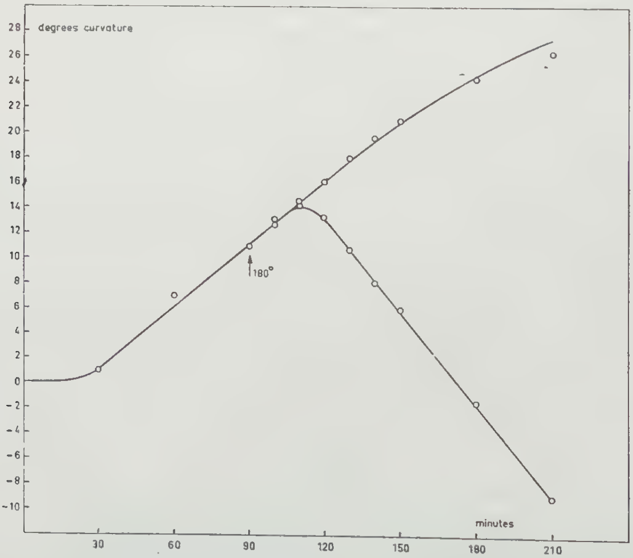

Fig. 8. Curvature of decapitated coleoptiles in a growth-substance solution (0.1 mg IAA/l). Upper line: controls kept in the same position for the entire experiment; lower line: rotated through 180° after 90 minutes.

period, and not rotated through 180°. The same was done with non-decapitated coleoptiles kept in water: after 10, 20 and 90 minutes they were rotated through 180°, while the control coleoptiles were kept in the same position for the entire experimental period.

The curvatures were measured at short intervals so that the curving rate could be determined accurately. Each experiment was repeated four or five times, and the values given in the results are the averages of these experiments. The results are shown in Figs. 8, 9, 10, 11, 12, 13 and 14.

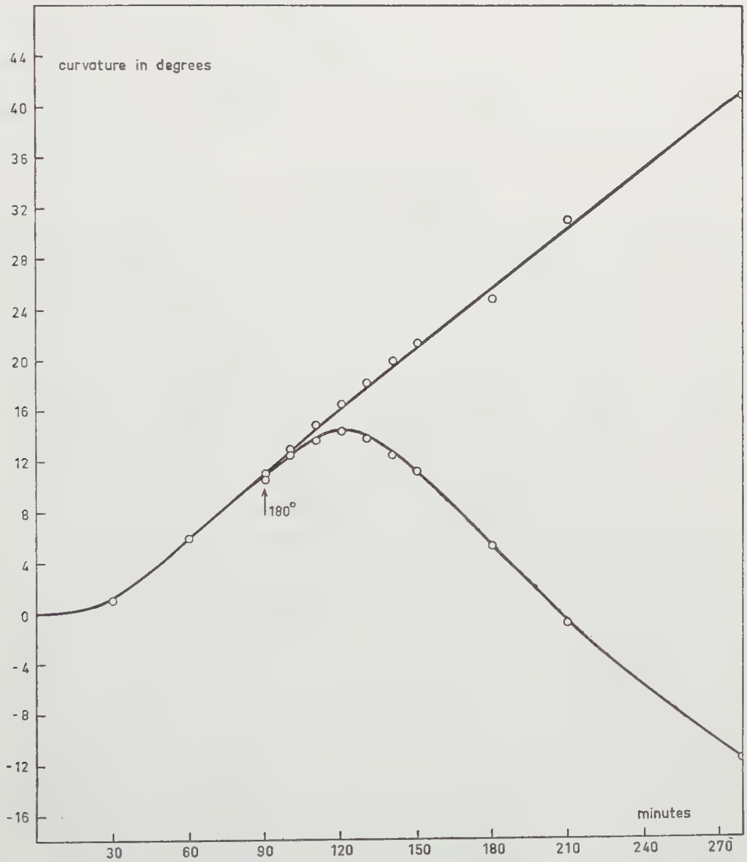

Fig. 9. Curvature of non-decapitated coleoptiles in water. Upper line: controls, not rotated through 180°; lower line: rotated through 180° after 90 minutes.

From the results the rates of curvature were calculated, starting from that point in the curves where the progress curve becomes a straight line. For example, the data from Figs. 8 and 9 (coleoptiles rotated after 90 minutes) yield the following figures:

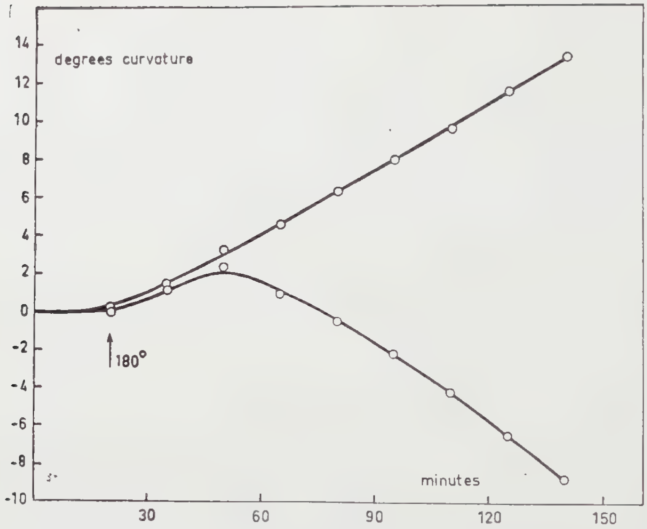

Fig. 10. Curvature of decapitated coleoptiles kept in a growth-substance solution (0.1 mg IAA/l). Lower line: rotated through 180° after 20 minutes; upper line: controls, not rotated through 180°.

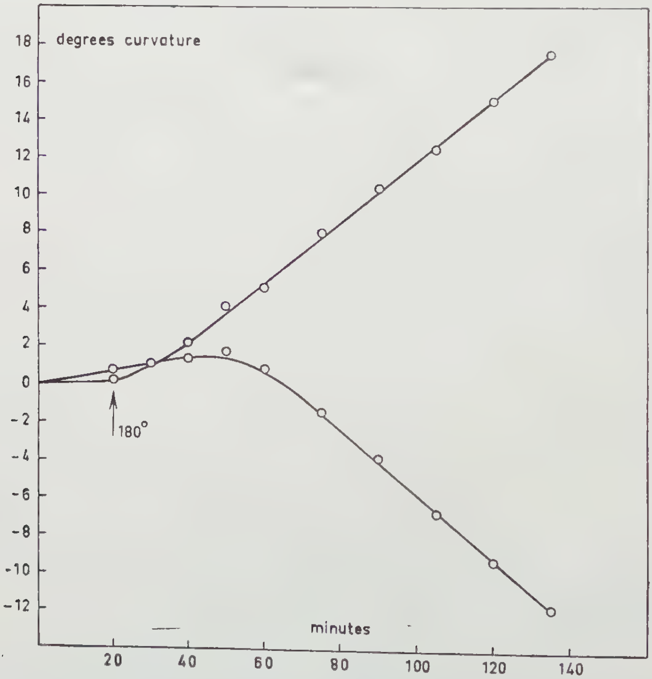

Fig. 11. Curvature of decapitated coleoptiles kept horizontally in a growth-substance solution (0.1 mg IAA/l). Upper line; controls, kept in the same position for the entire experiment; lower line: coleoptiles first kept vertically in the growth-substance solution for 30 minutes and then placed horizontally, first in one position and then rotated through 180° after 20 minutes.

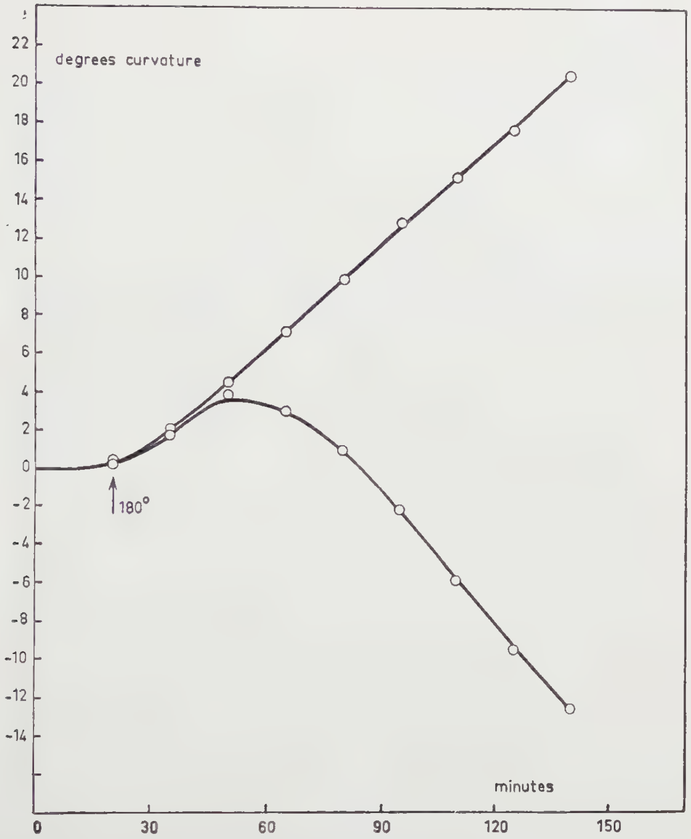

Fig. 12. Curvature of non-decapitated coleoptiles kept horizontally in water. Upper line: kept in the same position for the entire experiment; lower line: rotated through 180° after 20 minutes.

Decapitated coleoptiles:

Back curvature:
Curvature after 120 minutes . . . . : 13.2°
,, ,, 180 ,, ... : -1.3°
Rate of curvature . . . . : $\frac{14.5}{6}$
: 2.4°/10 min.

Original curvature:
Curvature after 60 minutes . . . . : 7.2°
,, ,, 180 ,, ... : 24.4°
Rate of curvature . . . . : $\frac{17.2}{12}$
: 1.4°/10 min.

Non-decapitated coleoptiles:

Back curvature:
Curvature after 130 minutes . . . . : 13.8°
„ „ 180 „ . . . . : 5.2°
Rate of curvature . . . . : $\frac{8.6}{5}$
: 1.7°/10 min.

Original curvature:
Curvature after 60 minutes . . . . : 5.9°
„ „ 180 „ . . . . : 24.8°
Rate of curvature . . . . : $\frac{18.9}{12}$
: 1.6°/10 min.

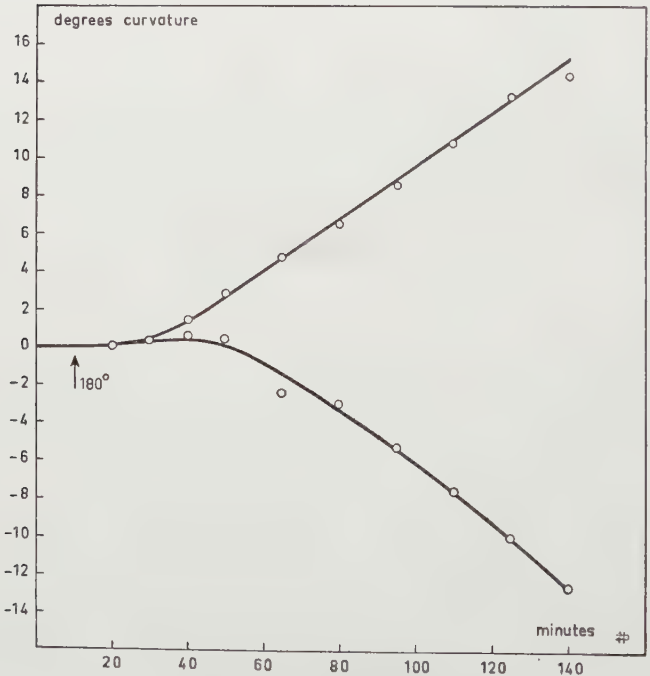

Fig. 13. Curvature of decapitated coleoptiles kept horizontally in a growth-substance solution (0.1 mg IAA/l). Lower line: rotated through 180° after 10 minutes; upper line: controls, kept in the same position for the entire experiment.

The rate of curvature in all experiments was calculated in the same way, and is given in Table IX.

From this table it can be seen that even under the same conditions the rate of curvature varies considerably. In the controls, the rate of curvature in the original direction of decapitated coleoptiles varied from 1.1°/10 minutes to 1.5°/10 minutes while in the case of non-decapitated coleoptiles the variation went from 1.6°/10 minutes to 2.4°/10 minutes. In all cases the rate of curvature of non-decapitated coleoptiles was higher than that of decapitated ones. The reason for these variations in the rate of curvature is not clear; they are most probably due to slight differences in the physiological condition of the coleoptiles.

In the case of decapitated coleoptiles there was an increase in the difference between the rate of the original curvature and the rate of the curvature in the opposite direction with the time that the coleoptiles had been kept in the first position. In the case of non-decapitated coleoptiles the largest difference was found with coleoptiles which had been kept horizontally for 20 minutes before rotation while with

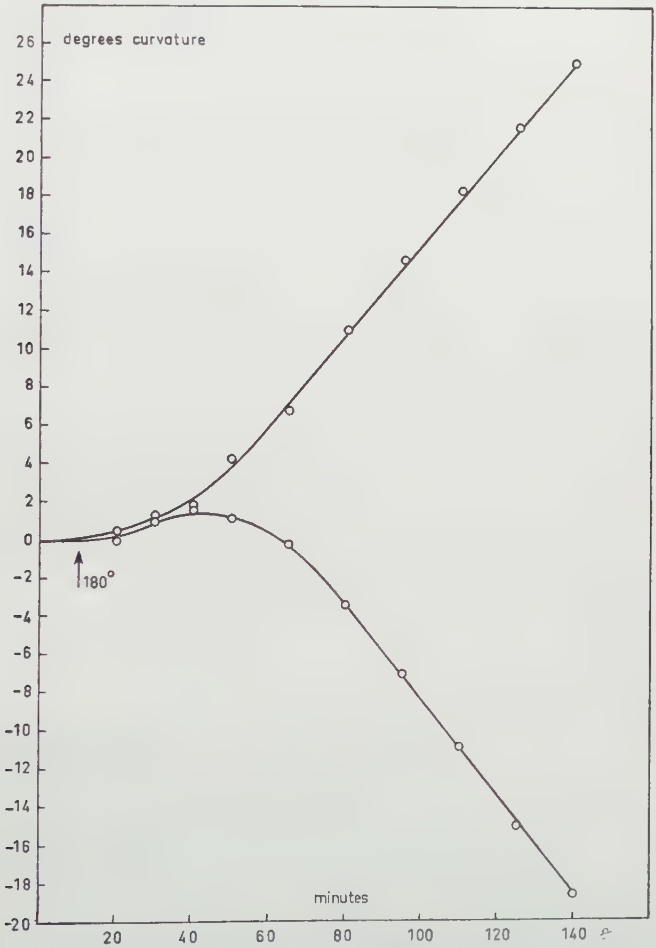

Fig. 14. Curvature of non-decapitated coleoptiles kept horizontally in water. Upper line: controls, not rotated through 180°; lower line: rotated through 180° after 10 minutes.

TABLE IX

Rate of curvature of non-decapitated coleoptiles in water and of decapitated coleoptiles in a growth-substance solution (0.1 mg IAA/l) before and after rotation through 180°.

Condition of coleoptile	Minutes horizontal before rotation through 180°	Rate of curvature in °/10 minutes	
		Controls	After rotation
Non-decapitated	10	2.4 ± 0.29	2.6 ± 0.18
	20	1.8 ± 0.09	2.3 ± 0.11
	90	1.6 ± 0.15	1.7 ± 0.09
Decapitated	10	1.2 ± 0.05	1.5 ± 0.09
	20	1.1 ± 0.07	1.2 ± 0.12
	20 *	1.5 ± 0.10	1.7 ± 0.12
	90	1.4 ± 0.07	2.4 ± 0.11

(* pretreated, i.e. coleoptiles kept vertically in the growth-substance solution for 30 minutes before being placed horizontally).

decapitated ones the largest difference was found when they had been kept horizontally for 90 minutes before rotation.

There are two possible reasons for this difference in the rate of curvature. The first is that, because of the curvature, the curving apical part of the coleoptile is not at an angle of 90° to the vertical when the coleoptile is rotated through 180°. It is possible that the induction is noticeably influenced by this angle and the induction would be greater in the second horizontal position. The other possibility is that the internal state of the coleoptile is changed during the first curvature in such a way that it would curve more easily in the opposite direction.

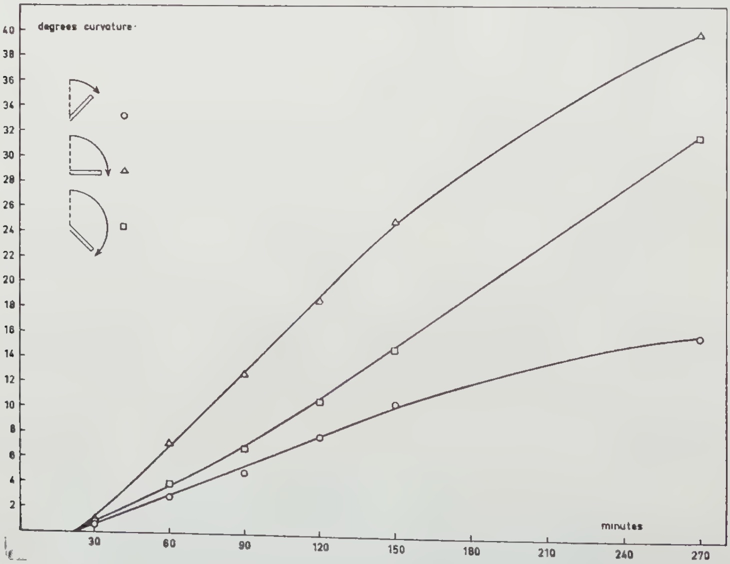

Fig. 15. Curvature of decapitated coleoptiles kept in a growth-substance solution (0.1 mg IAA/l) at angles of 45°, 90° and 135° to the vertical.

This is not the place to speculate on the different ways in which this might occur.

To investigate the first possibility, three sets of decapitated coleoptiles were kept in a growth-substance solution (0.1 mg IAA/l): one series at an angle of 45° to the vertical, the second series at an angle of 90° while the third series was kept at an angle of 135°. The three series were run simultaneously. The curvatures were measured at intervals of 30 minutes. The results are shown in Fig. 15. The same experiments were done with non-decapitated coleoptiles kept in water. The results of the latter are shown in Fig. 16.

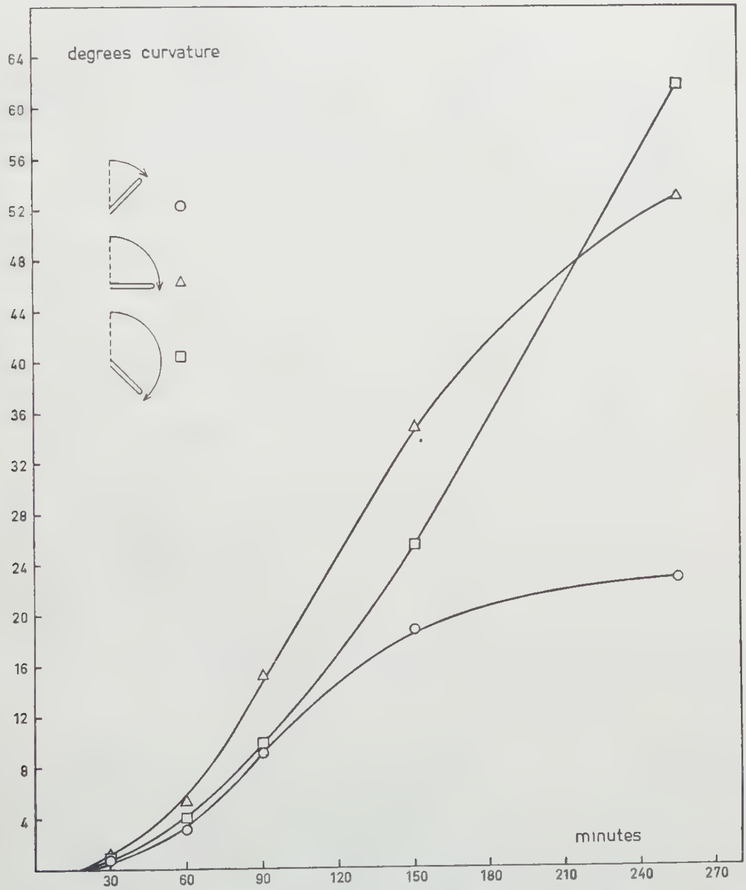

Fig. 16. Curvature of non-decapitated coleoptiles kept in water at angles of 45°, 90° and 135° to the vertical.

As was expected, the curvature of the coleoptiles that were placed at an angle of 90° to the vertical, was larger than that of the coleoptiles that were placed at an angle of 45° or of 135°. In the case of non-decapitated coleoptiles the curvature of those placed at 135° finally exceeded the curvature of those that were placed at 90°. This, however, did not take place before the former had reached a curvature of ± 45°, i.e. when they had reached the horizontal position. In the case of decapitated coleoptiles the curvature of those placed at 90° remained larger than that of the coleoptiles placed at 45° and 135° for the entire experiment. In view of the small differences between the positions before and after rotation in the experiments shown in Figs. 8—14, and the duration of those experiments, the increased rate at which the curvature in the opposite direction proceeds will not have been due to different angles to the vertical.

To investigate the second possibility, namely that the exposure to gravity had changed the reactivity of the coleoptile, the following experiments were performed: decapitated coleoptiles were kept horizontally in water for 60 minutes. After that, the experimental and the control series were placed in a growth-substance solution (0.1 mg IAA/l) but the experimental series was rotated through 180° while the control coleoptiles were left in the original position. The curvatures were recorded at intervals of 15 and 30 minutes and the results are shown in Fig. 17.

In the case of the coleoptiles which were not rotated through 180°,

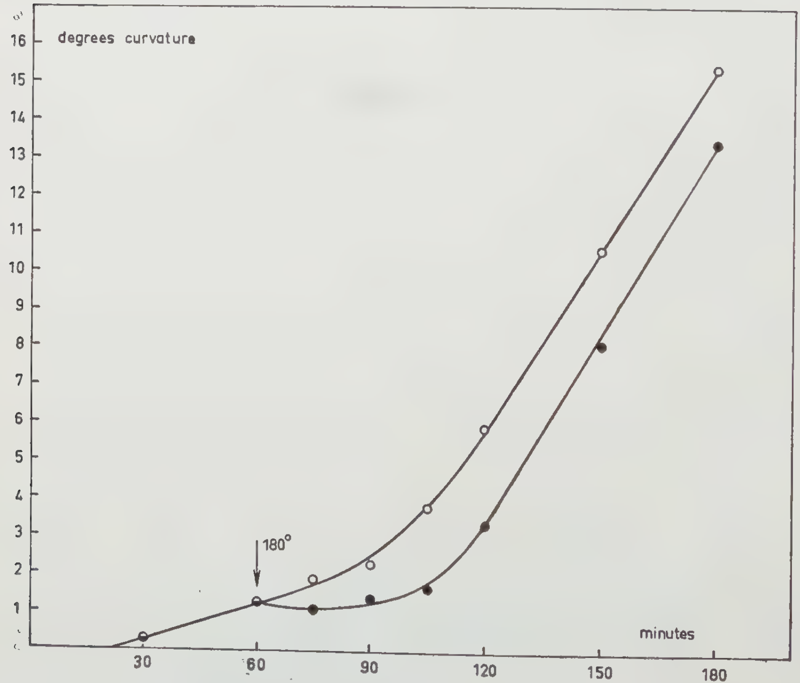

Fig. 17. Curvature of decapitated coleoptiles kept horizontally first in water for 60 minutes and then in a growth-substance solution (0.1 mg IAA/l) for the rest of the experiment. Circles: kept in the same position after addition of growth substance; dots: rotated through 180° after addition of growth substance. (In the latter case the progress curve has been reversed in order to facilitate comparison.)

the usual course of the development of the curvature was found. In the case of the coleoptiles which were rotated through 180° after remaining in water for 60 minutes, the curvature in the original direction was slight and lasted for 15 minutes only. The coleoptiles started curving in the opposite direction, and this curvature soon proceeded at the same rate as the control series and this rate too remained constant up to the end of the experiment. In this case there was definitely no increase in the rate of curvature of the coleoptiles rotated through 180° above that of the coleoptiles which were kept in the same position for the entire experiment. This leads to the conclusion that no changes took place in the coleoptiles during the time that they were kept horizontally in water, which would make them more receptive to the action of growth substance.

In another experiment, decapitated coleoptiles were kept in a growth-substance solution (0.1 mg IAA/l): for the first 90 minutes they were kept horizontally, and then for 30 minutes vertically. After that they were placed horizontally again, but in such a way that the former upper side then became the lower. The results are shown in Fig. 18.

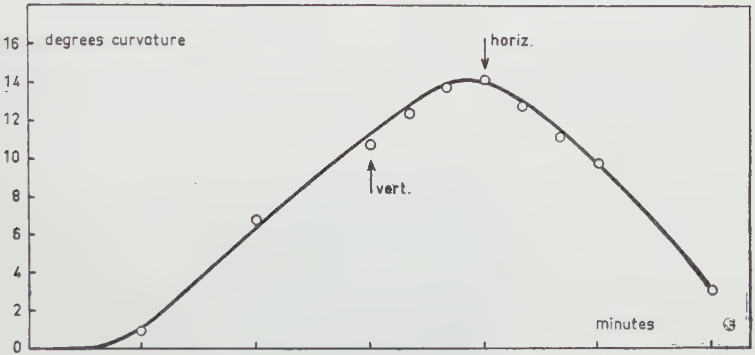

Fig. 18. Curvature of decapitated coleoptiles kept in a growth-substance solution (0.1 mg IAA/l). Coleoptiles kept horizontally for 90 minutes, then vertically for 30 minutes and then horizontally again in such a way that the former upper side became the lower side.

From these results the rate of the original curvature and the rate of the back curvature were calculated. The following was found: rate of original curvature: 1.6°/10 minutes; rate of the back curvature: 1.9°/10 minutes. The increased rate of the back curvature, therefore, is again apparent and its occurrence is not prevented by an interposed period in the vertical position.

The special point of the investigation in the latter part of this chapter was what might be the reason why the back curvature always proceeds more rapidly than the curvature in the original direction. Two possibilities were suggested and investigated: (i) the geo-induction is stronger when the coleoptiles are placed at an angle of more than 90° to the vertical and (ii) the internal state of the coleoptile is changed as soon as the coleoptile is placed horizontally, which changes make it more receptive and/or more reactive to an opposite induction.

The first possibility could be discarded (p. 34) and, as to the second possibility, one has to realise that the increased rate of curvature was only observed when it counteracted a curvature in the opposite direction. There was no increased rate of curvature when the coleoptiles had previously been in a horizontal position in which they could not take up growth substance and consequently did not receive any induction (Fig. 17).

This takes the problem from the field of geotropism into that of growth. The increased rate of curvature is apparently not caused by a factor of a specific geotropic nature but by the fact that the coleoptiles were curved. The mere fact that unequal growth has taken place in the opposite sides of the coleoptiles facilitates the process of straightening.

During the development of the back curvature the difference in the growth rate of both sides is larger than that present during the original curvature.

It is of no use to speculate here on the question whether this is due to an extra decrease of the ability to grow at the upper side or to an extra increase of this ability at the lower side. The solution has not to be sought in the direction of depletion of growth material only, since it must be taken into account that the rate at which the original curvature proceeds can remain constant for more than 3 hours (Fig. 9),

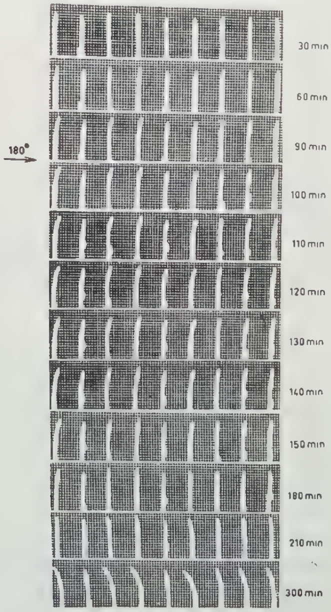

Fig. 19. Shadowgraphs of non-decapitated coleoptiles kept horizontally in water and rotated through 180° after 90 minutes. Note the straightening which proceeds from the base towards the tip and the complete absence of S-shaped curvatures.

and it only decreases, as it seems, by a decreased geo-induction due to a less favourable position of the apical part with respect to the direction of the gravitational force (Fig. 16).

Another feature which emerges from these experiments is the shape assumed by the coleoptiles—decapitated as well as non-decipatated ones—during the back curvature. Both the original and the back curvature start at the apical end and proceed towards the base. The back curvature, however, is preceded by a straightening of the coleoptiles, and this process starts at the base and proceeds towards the tip, just as in the case of geotropically curved coleoptiles when they are placed vertically (see p. 22). The back curvature does not start until the straightening of the coleoptiles has been completed. In only a few isolated cases an S-shaped curvature was found, that is, the tip of the coleoptile had started curving upwards before the coleoptile had completely straightened. The whole process of curvature in one direction, straightening and curvature in the opposite direction is shown in Fig. 19.

CHAPTER V

THE EFFECT OF ANTAGONISTIC GEOTROPIC EXPOSURES OF SHORT BUT EQUAL DURATION ON THE SUBSEQUENT DEVELOPMENT OF THE CURVATURE IN THE VERTICAL POSITION

In the preceding chapter the effect of antagonistic geotropic exposures on the rate of curvature was studied. After the coleoptiles had stayed in a horizontal position for some time, they were rotated through 180° and came under the influence of a geotropic exposure in the opposite direction. In those experiments the time of exposure in the two positions was not taken into account.

This chapter is concerned with the influence which two geotropic exposures in opposite directions for the same length of time exercise on the subsequent behaviour of the coleoptiles in the vertical position when they were placed in that position before any curvature became visible or at most had proceeded noticeably.

The procedure was as follows: non-decapitated coleoptiles were kept horizontally in water for exactly 10 minutes and then they were rotated through 180°. After 10 minutes in the second horizontal position, they were returned to the vertical and in that position shadowgraphs were made. A second experiment was performed, in which the coleoptiles instead of 10 minutes, stayed in the antagonistic positions for 20 minutes. The results are shown in Figs. 20 and 21 respectively.

The same experiments were also carried out with decapitated coleoptiles kept in a growth-substance solution (0.1 mg IAA/l). The times of exposure were here also 10 and 20 minutes respectively. A variation in this procedure was that the coleoptiles were kept vertically in the growth-substance solution for 30 minutes before the experiment started.

Here too this measure was taken in order to avoid that the amount of growth substance taken up by the coleoptiles during the 10 or 20 minutes before they were rotated through 180° would be insufficient. The results are shown in Figs. 21 and 22 respectively.

In the case of non-decapitated coleoptiles no curvatures were registered during the first 20 minutes. Only after the coleoptiles had been placed vertically the curvatures became visible. The coleoptiles began to curve in the direction of the first geotropic reaction; this curvature increased for about 20 minutes and then a counteraction set in; this

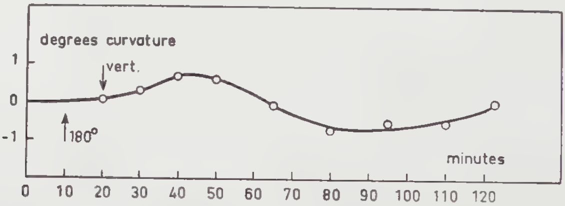

Fig. 20. Curvature of non-decapitated coleoptiles in water. Kept horizontally first for 10 minutes in one position and then rotated through 180°. After another 10 minutes returned to the vertical position.

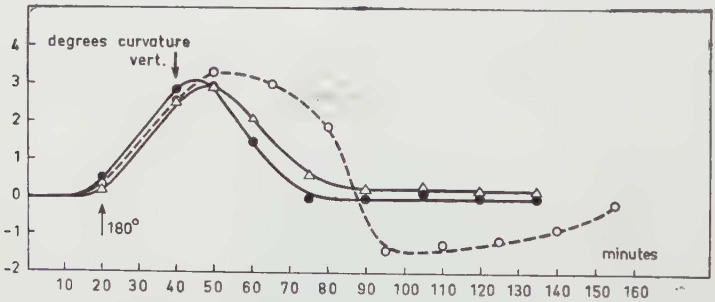

Fig. 21. Curvature of coleoptiles kept horizontally and after the first 20 minutes rotated through 180°. After another 20 minutes returned to the vertical position. Circles: non-decapitated coleoptiles in water; dots: decapitated coleoptiles in a growth-substance solution (0.1 mg IAA/l), previously kept vertically for 30 minutes in the same solution; triangles: decapitated coleoptiles in a growth-substance solution (0.1 mg IAA/l), not pretreated with growth substance.

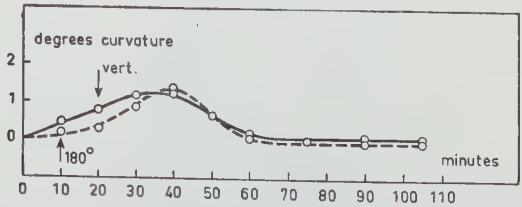

Fig. 22. Curvature of decapitated coleoptiles in a growth-substance solution (0.1 mg IAA/l). Placed horizontally first in one position and after 10 minutes rotated through 180°. After another 10 minutes placed vertically. Solid line: coleoptiles kept for 30 minutes in the growth-substance solution before being placed horizontally; broken line: placed horizontally without previous treatment with growth substance.

resulted first in a straightening of the coleoptiles and then in a curvature in the direction of the second geotropic reaction. Finally the coleoptiles became straight again. As could be expected, the curvatures were very small because in each position the geotropic exposure lasted only 10 minutes. It is evident, however, that both geotropic exposures caused a curvature, and that an opposing geotropic induction does not neutralize the reaction to the first exposure. When the geotropic inductions lasted 20 minutes, the same happened: during the 20 minutes that the coleoptiles were kept in the second position, they already started curving according to the original induction and after they had been placed vertically, this curvature still increased for about 10 minutes, after which the counteraction set in. After they had become straight, they also showed a slight curvature in the direction indicated by the second geotropic induction, and then they slowly became straight again.

In the case of decapitated coleoptiles, however, only a slight curvature in the original direction and a straightening of the coleoptiles were recorded. The coleoptiles did not curve according to the second geotropic exposure, not even when they had previously been kept for some time in the growth-substance solution.

The changes inside the coleoptile which are induced by the unilateral influence of gravity, are brought about within a relatively short time. This is proved by the fact that a curvature may make its appearance in the period in which an antagonistic geotropic induction has already set in. That the non-decapitated coleoptiles curved in both directions would seem to indicate that the changes are more rapidly induced by the gravitational force in the tip of the coleoptile than in the lower zones. In view of the fact that the tip is the production centre of auxin, and considering that the possibility of lateral distribution of this substance presumably decreases rapidly in the basal direction (Anker 1956), the above-mentioned difference in the behaviour of decapitated and non-decapitated coleoptiles is perhaps not so surprising.

CHAPTER VI

GENERAL DISCUSSION

The experiments reported in the preceding chapters yield information on several questions concerning the regeneration of a physiological tip, the uptake and fixation of growth substance, and the mechanism of the geotropic response in *Avena* coleoptiles. The geotropic response of decapitated coleoptiles strictly depends on the amount of growth substance that is available to the reacting tissue; this appears unambiguously in all experiments concerned. Since, in order to obtain geotropic curvatures in such coleoptiles, the latter have to be kept in growth-substance concentrations that are sub-optimal for straight growth (Anker, 1954, 1956), the development of such a curvature is a sensitive indicator for the presence (in a low concentration) of growth substance.

A. REGENERATION OF THE PHYSIOLOGICAL TIP

It has been shown that even in decapitated coleoptiles which have been separated from the seed, a certain regeneration of a physiological tip takes place. In a horizontal position the effect of this regeneration becomes apparent 2 to 3 hours after decapitation for at that time a marked increase in the rate of development of the geotropic curvature is noted. This time interval is the same as that found by SÖDING (1925, 1929), DOLK (1926), TENDELOO (1927), BEYER (1928), TSI-TUNG LI (1930) and WENT (1942) for the regeneration of a physiological tip in decapitated coleoptiles that have not been separated from the seed.

It is shown in this paper that growth substance taken up from solutions of sub-optimal concentration for straight growth (0.1 mg IAA/1), is fixed to, or utilized by the protoplasm within 30 to 45 minutes and cannot regulate the geotropism in a subsequent period. This means that, when isolated and decapitated coleoptiles start to curve geotropically in water after 2 hours, a slow production of growth substance continues at a constant level all the time. This result is well in line with SKOOG's statement (1937) that in deseeded, decapitated coleoptiles of *Avena* a slight formation of auxin occurs. The same was observed with deseeded and decapitated *Avena* coleoptiles by ARNAL and GEBHARDT (1955). The amount of precursor present in such coleoptiles is apparently sufficient to yield enough growth substance for a geotropic curvature to continue for at least 5 hours at a constant rate.

ARNAL and GEBHARDT (1955) observed that even in an IAA solution (1. 0 mg/l) after 10—16 hours a sudden increase in the growth rate occurs. In coleoptiles that are kept in water a similar increase sets in at the same time. The authors ascribe this increase to the regeneration of a physiological tip. They further conclude that this regeneration is not synonymous with a production of IAA since it was not only found in coleoptiles that were kept in water but also in those that were provided with IAA. As the change in growth rate occurred much later than normally, the regeneration of the physiological tip taking place, as a rule, 2 to 3 hours after decapitation, it is not unconceivable that it is due to some other cause, e.g. to stimulation either by the products of an autolysis or by products of bacterial origin.

In any case, one can conclude from the present experiments that in a medium containing IAA no regeneration of a physiological tip occurs. In long-lasting experiments in an IAA solution (0.1 mg IAA/l) the geotropic curvature of horizontally placed decapitated coleoptiles proved to proceed at a rate that remained constant for several hours. If a regeneration of a physiological tip should take place, this rate would either increase (external concentration sub-optimal) or decrease (internal concentration becoming supra-optimal), and this is not so. This suppression of regeneration by IAA might indicate that IAA is the auxin actually produced in the regeneration process since the equilibrium

$$\text{precursor} \rightleftarrows \text{growth substance}$$

will shift to the left in the presence of growth substance. On the other hand, it is possible that during growth the precursor is used up in other processes, as, from the work of THIMANN *et al.* (1951) it is known that during growth a qualitative change in the cell-metabolism occurs, the nitrogen metabolism included (see also BLANK and FREY-WYSSLING (1941)). It must be left to further experiments with other growth substances to check which of these explanations is correct.

B. THE UPTAKE AND FIXATION OF GROWTH SUBSTANCE

The uptake of growth substance from the external solution by the tissue of decapitated coleoptiles proved to be a rapid process. When, for instance, such coleoptiles were kept in a solution of growth substance (0.1 mg IAA/l) for 5 minutes only, they showed a geotropic curvature appreciably higher than that of controls kept in water. It appeared that the amount of growth substance taken up by the coleoptile increases with an increase in the time of growth-substance supply, up to 30 minutes. It would seem that after about 30 minutes a constant ratio is established between the rate of uptake (and basipetal transport) of growth substance and its fixation to, or utilization by the protoplasm. At this steady state a certain amount of growth substance appears to remain available for further activity, *in casu* the regulation of a subsequent geotropic curvature; this is the "free auxin".

From these data it follows that the rate of fixation or utilization of growth substance is slower than that of its uptake. At the steady state a certain amount of "free auxin" is available for further activity or for transport in a more basal direction. It further appears that the geotropic curvature after the coleoptiles have been transferred to water proceeds under such circumstances for 30 to 45 minutes. The development of this curvature is made possible by the growth substance already fixed in the horizontal position and by the "free" growth substance still available but also fixed within 30 to 45 minutes.

The work of REINHOLD (1954) indicates that in the uptake of auxin at least two components can be distinguished. BOTTELIER (1954), working with petioles of *Ageratum*, came to the conclusion that auxin, once it is taken up in the cells, is immediately fixed. JOHNSON and BONNER (1956), working on the uptake of 2,4-D (2,4-dichloro-phenoxy acetic acid), C^{14} carboxyl labelled, by coleoptile sections of *Avena*, came to the conclusion that two stages can be distinguished in the initial rapid uptake of 2,4-D, and that they are followed by a third kind of uptake. These stages are:

(1) a diffusion into the accessible part of the tissue, which is completed within 30 minutes. This part of the absorbed 2,4-D can freely diffuse out again;

(2) an exchangeable binding of 2,4-D, also completed within 30 minutes. This fraction cannot leach out from the tissue;

(3) a continuous uptake going on for hours. This 2,4-D cannot diffuse out and is not exchangeable.

As to stage (1) the present experiments yield no information. On the other hand, a time of 30 minutes was also found for the "binding" of the IAA, stage (2), but there are no data on the exchangeability of this binding. The fact that decapitated coleoptiles keep on curving when kept horizontally in a 0.1 mg IAA/l solution, whereas they stop curving after a while when they are transferred to water, is in favour of the continuous uptake, stage (3), described by Johnson and Bonner.

C. THE MECHANISM OF THE GEOTROPIC CURVATURE

As a variant on Went's almost classic slogan "without growth substance no growth" the phrase "without growth substance no geotropism" would be an apt expression of what the present experiments show. When it is realized that the faculty to develop a geotropic curvature is coexistent with that for straight growth, this is a trivial truth for the geotropic reaction.

Two kinds of experiments, however, clearly show that the unilateral gravitational force is "perceived" by the coleoptile only in the presence of growth substance. Decapitated coleoptiles, kept horizontally in water and then vertically in a growth-substance solution (p. 23) do not curve geotropically. This result is incompatible with that of an early experiment of BRAUNER (1923), in which decapitated coleoptiles were kept horizontally for 10 minutes and then provided with tips of coleoptiles which had been kept vertically; after that they developed a geotropic curvature. The results, however, are not very convincing. Similar experiments were made by CHOLODNY (1924) with decapitated roots and root tips, and in these experiments no curvatures were obtained. The results of Cholodny are well in line with those of the present experiments.

In other experiments (p. 13) decapitated coleoptiles were kept horizontally in water and then transferred in the same position to a growth substance solution in which they remained for 30 minutes. It appeared that nothing had been changed either in the receptivity or in the reactivity of the coleoptiles by the preceding exposure to gravity in the absence of IAA.

The experimental data, although indicating a direct dependence of the geotropic "perception" on the presence of growth substance in an available form, do not give any information on the nature of this process. An unequal lateral distribution of growth substance as a result of the unilateral action of gravity certainly offers an acceptable explanation, but leaves the question of the mechanism of this lateral shift of auxin unanswered.

Part of the present experiments indicate that growth substance once it has been taken up by the tissue is bound within 30 to 45 minutes and that it can no longer move freely about in the coleoptile. This is most clearly shown in the experiments in which decapitated coleoptiles had been kept horizontally in a growth-substance solution for a certain length of time, first in one position and then rotated through 180° (p. 24). In the latter position the reaction goes on for about 30 minutes in the original direction; this is the same time required for the curvature in the original direction to appear. Then only does the curvature in the opposite direction start. It appears therefore that the reaction made possible by the growth substance in the first horizontal position does not end at the moment of rotation through 180° and that the growth-substance molecules involved in this reaction cannot be mobilized in order to be utilized in a reaction according to the new orientation. This most clearly appears in the experiments where the coleoptiles were transferred to water at the moment of rotation. Therefore a curvature according to the new orientation can only be realized if free growth substance is available. This fact is not in contradiction with the theory of a lateral distribution of auxin by gravity, since the greater part of the growth substance is fixed and the free part is too small to cause a curvature. The fact, however, that the straightening of a curved coleoptile proceeds from the base towards the tip, should be explained in a different way and is perhaps due to the same type of growth-technical phenomena as mentioned below for the rate of the back curvature.

The effects of two short-lasting antagonistic exposures of equal duration (10 or 20 minutes) on decapitated coleoptiles kept in growth-substance solution and on non-decapitated coleoptiles kept in water, do not neutralize each other. In non-decapitated coleoptiles the curvature arising as a result of the second exposure is stronger than that which arises as a result of the first exposure. This, however, is in agreement with the conception that the tip of a coleoptile is more sensitive to "perceive" the gravitational force than the lower parts.

In these short-lasting exposures the exposure time approaches that which according to Rutten-Pekelharing (1910) is needed for a "just visible" curvature (50 % of the coleoptiles curved) namely 4 to 5 minutes. These short exposures to unilateral gravity are sufficient to elicit a geotropic reaction. This means that the lateral shift of the auxin transport, which is generally thought to be a preliminary step in the development of the curvature, should have proceeded to such an extent that as a consequence of a difference in the rate of growth of the lower side and of the upper side of the coleoptile a curvature is found.

Schrank (1944*a*) calculated that a transversal migration of an auxin-ion in a coleoptile by electrophoretic transport would take about 6 minutes. It is strange that it should take another 20 minutes before the difference between the growth of the lower and upper side is large enough to yield a visible curvature. Therefore not all questions with regard to the unequal distribution of growth substance by unilateral gravity, and with regard to the mechanism by which it is brought about, have as yet been answered.

Finally the phenomenon has to be discussed that after an antagonistic geotropic exposure of curved coleoptiles, the curvature according to the second exposure, the back curvature, generally proceeds at a somewhat higher rate than the original curvature. This phenomenon does not seem to be due to differences in geotropic induction (experiments in which coleoptiles were kept at angles of 45° and 135° to the vertical) nor to differences in geotropic sensitivity (Fig. 17), but must be due to growth-technical factors. The nature of the latter is still unknown but they certainly are not related to geotropism.

SUMMARY

1. The experiments described in this paper were performed with decapitated and non-decapitated *Avena* coleoptiles separated from the seed. They were immersed in water or in a growth-substance solution (usually 0.1 mg IAA/1). The geotropic response was studied with the aid of an apparatus similar to that described by Anker (1954).

2. Even in deseeded coleoptiles a regeneration of a physiological tip takes place, whose activity attains a constant though low rate after 2 to 3 hours and continues for at least 5 hours. In the presence of growth substance (0.1 mg IAA/1) in the external solution no regeneration of a physiological tip takes place.

3. In deseeded and decapitated coleoptiles the geotropic reaction as well as the geotropic perception are dependent on the presence of a growth substance, in this case IAA.

4. The uptake of growth substance is a rapid process, whereas the fixation of the growth substance to the protoplasm proceeds at a much slower rate. 30 to 45 minutes after its uptake in the cells all growth substance is bound. This means that, in the presence of growth substance, after about 30 minutes a steady state is established, i.e. an equilibrium between the rate of uptake, basipetal transport and fixation of growth substance, so that a certain constant amount of "free" growth substance remains available in the tissue.

5. In the absence of IAA no "preparatory processes" are induced by the unilateral influence of gravity in decapitated coleoptiles kept horizontally in water. For, if transferred into a growth-substance solution (0.1 mg IAA/1) and placed vertically, they do not curve and, if left horizontally after addition of IAA, they do not curve faster than coleoptiles which at the moment of growth-substance addition are given an antagonistic geotropic induction.

6. If an antagonistic geotropic induction is given to curved coleoptiles, the back curvature proceeds at a higher rate than the curvature in the original direction. It appeared that this was not due to the higher value of the angle between the tip and the vertical at the moment of rotation through 180°, but is caused by "growth-technical" rather than by specific geotropic factors.

7. When horizontally placed coleoptiles (in growth substance) are either put vertically or rotated through 180° the development of the curvature according to the first geo-induction proceeds for ca. 30 minutes. This is apparently due to: (1) the IAA is fixed during the first induction and is no longer available and (2) the concentration of the free auxin is too low to cause a curvature in the opposite direction. The straightening of geotropically curved coleoptiles after an antagonistic induction starts at the base and proceeds acropetally.

8. Two short-lasting antagonistic exposures (10 or 20 minutes) do not neutralize each other. They induce two subsequent reactions. With non-decapitated coleoptiles the second reaction is stronger than the first and than that of decapitated coleoptiles in a growth-substance solution. This indicates a particular ability of the coleoptilar tip to regulate geotropism.

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TWO NEW SPECIES OF HYDROCHARITACEAE

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(*Foundation Flora Malesiana, Leyden*)

(*received January 5th, 1957*)

During the precursory study of the *Hydrocharitaceae* of Malaysia for the Flora Malesiana two new species have been found among indetermined material.

Halophila linearis n. sp.—Fig. 1.

Caules tenues, sat fragiles, nodis radiculam singulam emittentibus, internodiis 1–2 cm longis; squamae translucidae, ellipticae-obovatae, apice obtusae vel rotundatae, marginibus integris, 3–4 mm longae; folia e axi laterali haud vel vix evoluta bina, linearia obtusa glabra, apice minute serrulato excepto marginibus integris, costa conspicua in utroque latere nervo marginali in folii apicem confluente comitata, venulis transversis nullis, 17–25 × 1 mm; petiolus evaginatus $^1/_2$–$1^1/_2$ cm longus. Flores et fructus ignoti.—Typus: Herb. Moss 20552 (BM).

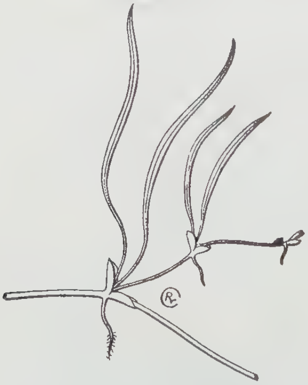

Fig. 1. *Halophila linearis* Den Hartog, nat. size (type)

AFRICA. Portug. E. Africa: Inhaca Isl., W. coast exposed at spring-ebb-tide, July 1931, Herb. Moss 20552 (BM).

Notes. This species differs from the others of sect. *Barkania* (Ehrenb.) Aschers. by its grass-like habit and the absence of cross-veins in the leaves. It resembles the African *H. stipulacea* (Forsk.) Aschers. by the serrulate apex of the leaf blades, but is well distinguished from it by the characters just mentioned and by the unsheathed petiole and small transparent scales.

Blyxa novoguineensis n. sp.

Dioica, caulescens, ramosa; folia spiraliter disposita, sessilia, semi-amplexicaulia, linearia, apicibus attenuatis, marginibus minute dentatis, 6–8 cm longa, 2–3 mm lata, nervo centrali prominente, nervis 6–8 parallelis inconspicuis, nervis transversalibus tenuissimis eos conjungentibus. Pedunculus axillaris, 0,5–18 cm longus, in anthesi evolutus. Spatha tubulosa, apice bifido, obtuso 2,5–4 cm longa, flores masculos 5–8 gerens; pedicelli 5–7 cm longi; sepala lineari-lanceolata, uninervia, viridia, prope apicem macula obscura praedita, apicibus acutis, 4–5 mm longis, 1,5 mm latis; petala 12–15 mm longa, 1 mm lata; stamina 9, filamentis 2–3 mm longis, antheris lineari-lanceolatis, apicibus acuminatis, 1,5–2 mm longis, 0,25–0,33 mm latis; rudimenta carpellorum 3, ovata, 1 mm longa, stylodio gracili, 2,5–3 mm longo. Plantae femineae ignotae.—Typus BRASS 7638 (L).

NEW GUINEA. Papua. Middle Fly River, very abundant in lake Daviumbu, in water 1–1 $^1/_2$ fathoms deep, Sept. 1936, L. J. Brass 7638 (L, BO).

Notes. The new species belongs to sect. *Caulescentes* which is characterized by the caulescent habit. It differs from the two other species of this section by the following characters: flowers dioecious, stamens 9, spathe long-peduncled.

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REVISION OF THE GENUS POLYCARPAEA (CARYOPH.) IN MALAYSIA

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(*received November 28th, 1956*)

The genus is extremely poorly represented in the Malaysian area as compared with the wealth of species described from the African flora and with the relatively large number of species described from Asia and Australia. Most of the specimens collected in Malaysia belong to the widely distributed *P. corymbosa* (L.) Lamk, which is still of very limited occurrence in Malaysia. A Queensland species, *P. spirostylis* F. v. M., has once been reported from islands in Torres Straits.

The three other species are apparently local-endemics from the climatically dry Lesser Sunda Islands and I have been unable to match them with any of the described species from the Asiatic and Australian floras.

As the species of *Polycarpaea* are very similar in habit and vegetative characters, stress is laid upon clearly distinguishable flower details. In descriptions one should be careful in dissecting flowers: petals and stamens are connate only in sect. *Planchonia*; in herbarium specimens of other species they may stick sometimes together but are really free.

The stamens are in some species inserted on a scarious ring; the petals are inserted on this ring at the outer side. The parts of this ring just opposite the petals can develop into very minute, triangular acute or scale-like staminodial appendages, as is the case in sect. *Aylmeria*. These staminodes are easily overlooked, as must have been the case in the well-known widely distributed *P. corymbosa* [1]), in which species I found minute, transversely rectangular or scale-like appendages opposite the petals, between and connate with the stamens. It is difficult to decide whether these minute organs are definitely homologous with staminodes or not. It may be that they are just parts of the scarious ring but occupy exactly the position where staminodial vestiges should be found. Possibly the presence of these staminodial appendages is not so valuable in the genus; if these organs have to be interpreted as staminodes, however, then *P. corymbosa* should, in my opinion, be transferred to sect. *Aylmeria*.

In *P. spirostyles* (§ *Planchonia*) and *P. sumbana* (§ *Polycarpaea*) staminodes are absent; in *P. zollingeri* and *P. timorensis* they are present, though of minute size and sometimes hardly visible.

In the description the term "petals" has for convenience's sake been applied to the organs of the whorl succeeding the sepals. It has been demonstrated by MATTFELD (in FEDDE, Rep. Beih. 100, 1938, 147–164) that in the *Caryophyllaceae* the "petals" represent in all probability an outer whorl of staminodial nature and no true petals. Mattfeld considers the episepalous stamens with their (often present) staminal glands as tangentially split phyllomes homologous with the alternisepalous stamens with their "petals". Such a split phyllome consists of a stamen and two dorsal, mostly connate, stipules (staminal gland(s) or "petal(s)". In the Malaysian species of *Polycarpaea* the glands of the episepalous stamens are absent, and of the whorl consisting of alternisepalous stamens with their accompanying "petals" the stamens are reduced to staminodes (§ *Aylmeria*) or absent.

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[1]) And in the Indo-Chinese *P. stylosa* Gagnep. which is closely related to *P. corymbosa*.

The material on which this revision has been based is contained in the Herbarium Bogoriense and the Rijksherbarium. Of *P. zollingeri* (Fenzl) Bakker material was obtained from the Muséum d'Histoire Naturelle, Phanérogamie, Paris and Papuan material of *P. spirostylis* F. v. M. was borrowed from the Melbourne Herbarium. Sincere thanks are due to the directors of these Herbaria.

Polycarpaea Lamarck

Annual or perennial, dichotomously branched herbs, sometimes woody at the base. Leaves opposite, often with developed axillary buds which give the impression of the presence of (false) whorls. Stipules scarious. Inflorescences poor or rich-flowered cymes provided with scarious bracts. Sepals scarious, not keeled. Petals (by Mattfeld interpreted as staminodes) structurally similar to the sepals, but frequently toothed at the apex, sometimes (§ *Planchonia*) to varying degree connate mutually and with the filaments. Stamens 5 (or less), sometimes (§ *Aylmeria* alternating with 5 minute staminodes. Style simple, stigma punctate to globular, or lobed. Capsule 3-valved.

KEY TO THE MALAYSIAN SPECIES

1. Petals connate in their lower half into a tube or cup (§ *Planchonia*) . . . . 1. **P. spirostylis**
1. Petals free, at the base annularly adnate to the stamens (and staminodes if present).
    2. Sepals with a c. ½ mm broad, 3-nerved, pubescent, greenish median band not reaching the apex . . . . 4. **P. zollingeri**
    2. Sepals almost entirely scarious or with a narrow glabrous purple midrib of various length.
        3. Midrib of the sepals reaching up to c. 1–1½ mm below the apex. Petals narrowly oblong, c. 2½–3 by ½–¾ mm. Anthers oblong, c. ½ mm. Style c. 1¼–2 mm. . . . . 3. **P. sumbana**
        3. Midrib of the sepals absent or only visible at the base over c. 1 mm. Anthers orbicular, c. ⅙–⅕ mm. Style ⅛–½ mm.
            4. Sepals without a true midrib. Petals very small, c. ½–1 mm long, top not bifid . . . . 2. **P. corymbosa**
            4. Sepals with a midrib, visible at the base over 1mm. Petals larger, c. 1¼–2 mm long, top often bifid. 5. **P. timorense**

1. **Polycarpaea spirostylis** F. v. M. Rep. Bab. Exp. (1858) 8; Bth. Fl. Austr. 1 (1863) 165; F. v. M. Descr. Not. Pap. Pl. 2 (1886) 43; Bailey, Queensl. Fl. pt 1 (1899) 91; Domin, Bibl. Bot. Heft 69 (1925) 653.

Annual, c. 20–30 cm high. Stems slender, erect, glabrous. Internodes 2–2½ cm. Leaves sessile, linear c. 10–20 mm long, 1 mm broad, glabrous; apical mucro c. ½ mm. Stipules small, ovate-oblong, c. 1½–2 mm long, top acuminate. Capitate cymes many-flowered, c. 3½ cm diam. Bracts ovate-oblong, boat-shaped, brownish striate, c. 3 by 1¼ mm, with a distinct midrib; top acute and lacerate; margin serrate; axil with some long soft hairs. Pedicels less than 1 mm long, flowers almost sessile. Sepals 5, scarious, ovate-oblong, acute, c. 6 by 2 mm; midrib disappearing c. 2 mm below the top. Petals 5, scarious, in their lower part connate with the stamens into a tube of c. 3½ mm; free slips entire, oblong-triangular with a rounded top, c. 1½ mm, curled outward. Stamens somewhat longer than the petals, filaments c. 5 mm, free parts c. 1½ mm; anthers broad elliptic, c. ⅔ mm long. Ovary very

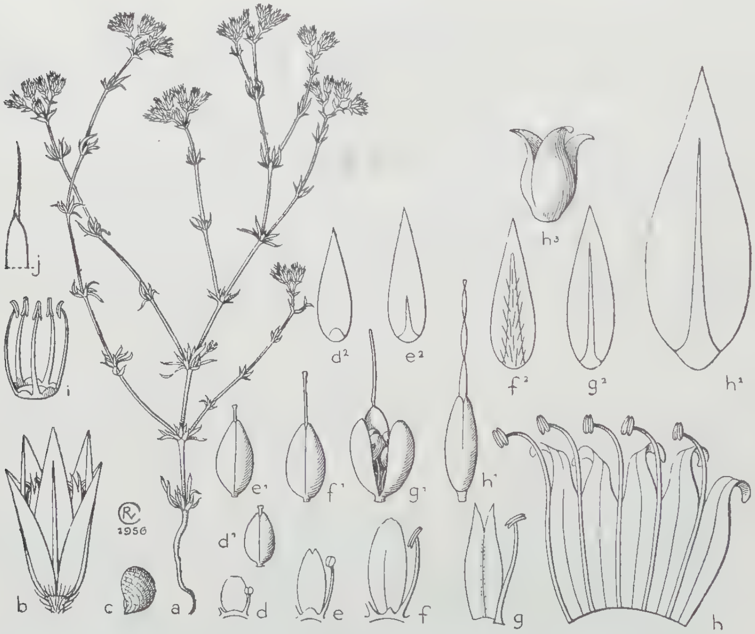

Fig. 1. Details of the five Malaysian species of *Polycarpaea*. a. Habit of *Polycarpaea sumbana* Bakker, nat. size (Iboet 51), b. flower, × 6, c. seed, × 13, — d, d¹, d², *P. corymbosa* (L.) Lamk, respectively showing in d. structure and insertion of stamen and staminal ring with petal, d¹. fruit, d². petal with indication of the non-scarious portion of the midrib, all × 6 (Curran & Merritt FB 16545), — e, e¹, e², *P. timorensis* Bakker ditto, × 6 (Walsh 351), — f, f¹, f², *P. zollingeri* (Fenzl) Bakker, ditto, × 6 (Zollinger HZ 1096), — g, g¹, g², *P. sumbana* Bakker, ditto, × 6 (Iboet 51), — h, h¹, h², *P. spirostylis* F. v. M., ditto, h³. dehisced fruit, all × 6 (Hartmann in Melb.), — i. *P. timorensis* Bakker, stamens with staminal ring, × 10, — j. *P. zollingeri* (Fenzl) Bakker, leaf tip, × 6.

shortly stipitate, oblong, c. 2 mm, tapering at the top into a long spirally twisted caducous style c. 3 mm long; stigma punctiform. Capsule c. 1 mm stalked, ovate, c. 2–3 mm long, brown, when ripe, opening at the top with 3 triangular, recurving valves.

Distr. Queensland, Islands of Torres Straits, C. Hartmann, not yet reported from Papua proper.

This species is in Queensland renowned for its value as indicator of copper deposits and is frequently used by practical miners as a guide to that mineral (Bailey l.c.) a quality apparently shared with *P. glabra* White (Proc. R. Soc. Queensl. 37, 1926, 153).

Note. The specimen described above differs distinctly from the description in Bentham's Fl. Austr. It shows stems which are not woody at the base, shorter filaments, and a much smaller capsule. Domin, however, states that *P. spirostylis* is a very variable species. Another specimen from Australia (Winders 7397) differs in having bifid petals and filaments only slightly longer than the petals. I refrain from accomodating the Torres Straits specimen in a new infraspecific taxon.

2. **Polycarpaea corymbosa** (L.) Lamk, Tabl. Encycl. 2 (1797) 129; W. & A. Prod. (1839) 90; Bth. Fl. Austr. 1 (1863) 166; Hook. f. Fl. Br. Ind. 1 (1874) 245; F.-Vill. Nov. App. (1880) 15; Bailey, Queensl. Fl. 1 (1899) 92; Merrill, Philip. J. Sc. 5 (1910) Bot. 347; Domin, Bibl. Bot. Heft 69 (1925) 100; Merrill. En. Philip. 2 (1923) 139 — *Achyranthes corymbosa* Linne, Sp. Pl. (1753) 205.

Annual, c. 12–40 cm high. Stems slender, erect, pubescent; internodes c. 1–4 cm. Leaves sessile, linear, mostly c. 10 mm, but up to 20 mm long, less than 1 mm broad, glabrous; apical mucro c. $\frac{1}{2}$–1(–2) mm. Stipules ovate-oblong, c. 3–4 mm long, the c. 1 mm filiform apex included, c. 1 mm broad; margin not quite entire. Cymes rather dense, c. 2–6 cm diam. Bracts triangular-ovate from a truncate, stem-clasping base, c. 2–$2\frac{1}{2}$ by 1–$1\frac{1}{2}$ mm; top acute and lacerate with a few linear slips. Pedicels of the terminal flowers c. 2 mm, of the other flowers c. 1 mm or less, pubescent. Sepals 5, scarious, ovate-oblong, c. $1\frac{1}{2}$–3 by $\frac{2}{3}$-1 mm; midrib hardly visible in the basal $\frac{1}{6}$ part as a dark-coloured or -striate spot. Petals 5, scarious, brownish, narrowly elliptic to almost orbicular, very small, c. $\frac{1}{2}$–1 mm. Stamens shorter than the petals, inserted on a scarious ring; anthers orbicular, c. $\frac{1}{6}$ mm. Staminodes oppositipetalous, very minute and hardly visible, perhaps only parts of the scarious ring. Ovary almost globular, very small, c. $\frac{1}{2}$ mm; style very short, c. $\frac{1}{6}$–$\frac{1}{8}$ mm; stigma 3-lobed. Capsule elliptic, 3-valved, c. 1–$1\frac{1}{2}$ by $\frac{1}{2}$–$\frac{3}{4}$ mm, brown. Seeds c. 6, reniform, yellowish-brown, c. $\frac{1}{3}$ mm.

Distr. In the tropics from Africa to Australia, in Malaysia only known from the following localities.

Lesser Sunda Islands: P. Kisar, inland place E. of Wonreli, secondary vegetation, 5–200 m, Bloembergen 3879 (L).

Moluccas: Sula Isl., Taliabu, kampong Kapa: Atje (Exp. Hulstijn) 89 (BO,L).

Philippines: Luzon, Benguet Prov.: Curran & Merritt FB 16545 (L), Ramos & Edaño BS 37936 (BO); Merrill 4392 (BO,L); Ramos BS 5803 (BO,L). Mindanao: Cotabato Prov., Ala Valley, weed in rice fields, 1–1½ ft. tall, fls. silvery: J. V. Santos 4806 (L).

Open dry sandy places, dry slopes, etc. from sea-level up to c. 1300 m; locally sometimes abundant.

3. **Polycarpaea sumbana** nov. sp. (§ *Polycarpaea*).

Annua, c. 8–15 cm alta. Caulis tenuis, erectus, basi saepe ramosa, dense crispato-pubescens, glabrescens; internodia c. 1–2 cm. Folia sessilia, linearia, plana, sparse pubescentia, apice acuta mucrone c. ½ mm longo, 3–6 × ¾ mm, costa indistincta. Stipulae scariosae ovato-oblongae, acutae, apice irregulariter fimbratae, c. 2½ × ¾ mm. Innovationes axillares frequenter adsunt. Cymae plerumque densae, c. 1–2 cm diam. Bracteae scariosae, basi semi-amplexicaules, ovato-ellipticae, acute-acuminatae, margine minute serratae, c. 2½–3 × 1½ mm. Pedicelli 1 mm. Sepala 5, scariosa, ovato-oblonga, acuta, glabra, c. 3–4½ × 1–1½ mm, costa firma c. 1–1½ mm infra apicem evanescente. Petala 5, scariosa, libera, anguste oblonga, uninervia, c. 2½–3 × ½–¾ mm, apice 2-dentata, raro subdentata, dentibus ⅓–½ mm longis. Stamina 5, basi cum petalis in annulum conjuncta, libera, c. 2½–3 mm longa. Antherae c. ½ mm longae. Staminodia desunt. Ovarium ellipsoideum, c. 1–1¼ × ½ mm. Stylus filiformis, 1½–2 mm longus; stigma punctiforme. Capsula 3-valvata, ellipsoidea, c. 1¾ × ¾ mm. Semina c. 8, minuta, c. ½ × ¼ mm, subreniformia, dilute brunnea.

Distr. Endemic in the Lesser Sunda Islands.

Lesser Sunda Islands: E. Sumba, Mambesu, Iboet 51 (BO;L, type); Waikelo, Iboet 357 (BO), common dry limestone, conspicuous by its silvery appearance, 200 m, De Voogd 1993 (BO,L); Waingapu, cattle range subject to annual burning, 200 m, Monod de Froideville 2046 (BO,L), in pasture on shallow soil, fls. carmine red, Monod de Froideville 1331 (BO). P. Savu, on the coast between *Pandanus*. Bloembergen 3282 (BO,L).

4. **Polycarpaea zollingeri** (Fenzl) comb. nov.—*Aylmeria zollingeri* Fenzl ex Zoll. Syst. Verz. (1855) 141, nomen nudum; Nat. Tijd. Ned. Ind. 14 (1857) 163, descr.

Annual. Stems slender, erect, pubescent; internodes c. 1–1½ cm. Leaves sessile, narrowly elliptic to linear, 2–7 mm long and 1–2 mm broad, pubescent; apical mucro c. 1–2 mm. Stipules narrowly ovate-oblong, incl. the thread-like apex c. 4 by ¾ mm; top c. 2 mm thread-like acuminate; margin not quite entire. Cymes rather dense, c. 1½–3 cm diam. Bracts triangular-ovate with a truncate, stem-clasping base, c. 2½–3 by 1–1½ mm; top acute and lacerate with a few linear slips. Pedicels c. 1 mm, pubescent. Sepals 5, scarious, ovate-oblong, acute, c. 3½–4 by 1 ⅓ mm; central part c. ½ mm broad, herbaceous, appressed-hairy, disappearing c. 1 mm below the top, containing 3 anastomosing nerves, greenish. Petals 5, scarious, oblong-elliptic, top blunt and slightly erose or bifid, c. 1½–2½ by ⅔–1 mm; midrib clearly discernable, disappearing c. 1 mm below the top. Stamens 5; filaments free, connate at the base with the petals and the staminodes, c. 1–2mm; anthers oblong, c. $\frac{1}{2}$–$\frac{2}{3}$ mm long. Staminodes oppositipetalous, very minute, triangular-acute, or composed of faint lobes and hardly visible. Ovary ellipsoid, c. 1 by $\frac{1}{2}$–$\frac{1}{3}$ mm; style slender, c. $\frac{1}{2}$–$1\frac{1}{2}$ mm; stigma punctate. Capsule ellipsoid, 3–valved, c. 2 by 1 mm, the upper part brownish-striate. Seeds numerous, reniform, light brown, with dark brown spots, c. $\frac{1}{3}$–$\frac{1}{2}$ mm.

Distr. Endemic in the Lesser Sunda Islands.

Lesser Sunda Island: Sumbawa, Bima district, Mt Tambora, sandy places between 600 and 1800 m, fl. Aug., Zollinger HZ 1096 (BO; P, type). Flores, Endeh, common in a coconut plantation, fl. June, Rensch 973 (BO).

Note. The specimen Rensch 973 differs slightly from the type in having bifid petals and a shorter style ($\frac{1}{2}$ mm instead of $1\frac{1}{4}$–$1\frac{1}{2}$ mm).

5. **Polycarpaea timorensis** nov. sp. (§ *Aylmeria*).

Annua, c. 10 cm alta. Caulis tenuis, erectus, dichotomus, dense crispato-pubescens, glabrescens; internodia 1–2 cm. Folia sessilia, linearia, plana, 3–6 × $\frac{1}{2}$–$\frac{3}{4}$ mm, apice acuta, mucrone $\frac{1}{2}$–1 mm longo; costa indistincta. Stipulae scariosae, uninerves, oblongae, 2 × $\frac{3}{4}$ mm, acutissime acuminatae, margine irregulariter incisae. Cymae densae, 1–2 cm diam. Bracteae convexae, scariosae, basi semi-amplexicaules, ovato-oblongae, uninerves, acutae, 2–$2\frac{1}{2}$ × 1–$1\frac{1}{2}$ mm, margine irregulariter incisae. Pedicelli 1–2 mm. Sepala 5, scariosa, ovato–oblonga, acuta, glabra, c. 3 × 1 mm; costae pars conspicua 1 mm longa. Petala 5, scariosa, uninervia, libera, elliptico-oblonga, c. $1\frac{1}{4}$–2 × $\frac{1}{3}$–$\frac{3}{4}$ mm, apice late rotundata, bidentata, vel irregulariter dentata. Stamina fertilia 5, basi cum petalis et staminodiis in annulum conjuncta, libera, c. $1\frac{1}{2}$ mm, antheris c. $\frac{1}{5}$–$\frac{1}{4}$ mm, orbicularis. Staminodia 5, scariosa, squamiformia, oppositipetala, minuta. Ovarium ellipsoideum, c. $\frac{2}{3}$ × $\frac{1}{2}$ mm; stylo brevissimo $\frac{1}{3}$–$\frac{1}{2}$ mm longo, stigmate trilobo. Capsula brevissime pedicellata, ellipsoidea, 3–valvata, c. $1\frac{1}{2}$–2 × $\frac{2}{3}$–1 mm Semina c. 6, reniformia, c. $\frac{1}{2}$ mm.

Distr. Endemic in the Lesser Sunda Islands.

Lesser Sunda Islands: W. Timor, Nenas, Mt Mutis, rare, 1250 m, M. E. Walsh 351 (BM, BO; L, type).

EXCLUDED

Polycarpaea frankenioides Presl, Rel. Haenk. 2 (1831) 6; F.-Vill. Nov. App. (1880) 15 is according to Merrill (En. Philip. 2, 1923, 135), who examined an original specimen in the Prague Herbarium, conspecific with the Aizoaceous *Glinus oppositifolius* (L.) DC.

Polycarpaea marginata Presl, Abh. Böhm. Ges. Wiss. V, 3 (1845) 571, repr. 141 = *Polycarpon indicum* (Retz.) Merr. Philip. J. Sc. 10 (1915) Bot. 302; En. Philip. 2 (1923) 139.—The reduced species was based on an Indian specimen (Helfer 303) and was not mentioned in the Flora of British India. From Presl's description it is clearly referable to *Polycarpon indicum*.

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POPULUS CANADENSIS MOENCH VERSUS P. EURAMERICANA GUINIER

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(*received December 18th, 1956*)

Considerable difficulties have arisen recently in the nomenclature of the trees which, in Europe anyhow, are known as "Canadian Poplars". Since many years we have been accustomed to use for this taxonomical group the name *Populus canadensis* Moench, but the International Poplar Committee of the F.A.O. has substituted this name by *P. euramericana* Guinier. In modern poplar literature, and especially in those publications that are destined for the practice, for example in descriptive lists of varieties, the name *P. euramericana* Guinier is increasingly used. For this reason it is definitely desirable to see in how far this name change is justified.

The Canadian Poplars in Europe widely planted were not introduced from Canada, and not even from North America. They are hybrids between the american *P. deltoides* Marshal and the european *P. nigra* L., of which the first ones originated spontaneously in France around the middle of the 18th century, a short time after *P. deltoides* has been introduced in Europe. *P. deltoides* itself seems to have disappeared soon afterwards, probable the cause was that the hybrids were more resistent than the american species against the european climate. Later, in the Netherlands in 1891, *P. deltoides* was once more imported from the U.S.A., and one particular clone of it is now rather frequently planted along the dutch roads as "Heidemij."

It seems that in the beginning the replacement of *P. deltoides* by the hybrids has escaped the attention, and this is easy to understand, as in the hybrids the character of *P. deltoides* generally dominates, so that they are very similar to the latter.

The oldest descriptions of the concerned poplars were given by Moench (1785) who published a catalogue of trees planted in the Weissenstein-park (now Wilhelmshöhe) at Kassel; in this catalogue he mentioned two species that are of importance to us, viz. *P. caroliniensis* and *P. canadensis*. He undoubtedly supposed that the first was an american species and the second one a Canadian poplar.

For a very long time it was not possible to give a correct interpretation of Moench's descriptions. The essential difference between *P. deltoides* and the hybrids was not known; even in 1928, at the International Forestry Congres held at Arnhem, nobody was able to answer the question what the differences between *P. deltoides* and the Canadian Poplars really are, (Houtzagers, 1937, 1). Nevertheless valuable literature was published about this subject, viz. HENRY (1913) who had given a detailed survey of the origin of the hybrids and REHDER (1923) who had argued that the correct name for these hybrids should be *P. canadensis* Moench. Due to insufficient knowledge the name *P. canadensis* has been used for different taxa of Populus, although mostly for segregates of the hybrids, e.g. for *P. serotina*, etc. To put an end to this confusion HOUTZAGERS (1937, 2) proposed to regard the name *P. canadensis* Moench as a nomen ambiguum, which means that it should never again be used. Acting upon this opinion GUINIER (1950) created a totally new name for the group of hybrids, namely *P. euramericana* and thus the hybrids are now known under two names, which causes a great confusion. The two points of view are strongly opposed: the nomenclature experts reject the name *P. euramericana* Guinier because it is illegitimate, whereas the International Poplar Committee accepts it as the only official name.

Therefore, it is necessary to examine which name is the correct one.

1. THE NAME P. CANADENSIS MOENCH

a. The diagnosis

Moench's catalogue is a rare book; by the good help from the librarian of the Kew herbarium I received a fotocopy of it. and afterwards I found that an important part of the catalogue has been republished as an appendix to a guide map of the Wilhelmshöhe-park (SAUER, 1955). Moench gives in his catalogue 10 poplar-species of which only the last two are of importance to us. Moench describes them as follows:

"POPULUS *caroliniensis*, foliis cordatis, crenatis, supra glandulosis, antice integris, Die Carolinische Pappel"
"POPULUS *Canadensis*, foliis cordatis, crenatis, eglandulosis, Die Canadische Pappel"

These descriptions are only short, but I think sufficient; the presence or absence of the glands at the upperside of the leave-base is decisive. There are no american poplars of the group of *P. deltoides* which lack these glands, and to identify *P. canadensis* with the balmpoplar, as was done by DODE (1905), is certainly incorrect, because the differences between these two species are already clearly brought out in Moench's list. *P. nigra* never has glands, and in the present day hybrids there are either two, one or no glands. Moreover MOENCH (1894) gives in a later publication further details; here he alters the name *P. canadensis* in *P. latifolia*, and describes the flowers and fruits, but that does not help us much, because in dealing with the american poplar, which he renamed *P. glandulosa*, he states that the flowers of this species do not differ from those of *P. latifolia*. Still he indicates that the twigs of *P. latifolia* are less pronounced 5-edged than those of *P. glandulosa*. Consequently it seems to me quite justified to identify on account of the data given in the diagnosis *P. caroliniensis* Moench with *P. deltoides* Marshal, and *P. canadensis* Moench with our canadian poplars,

b. The type

It is noteworthy that there is no reference at all in the literature with regard to type-material. Hoping to find some of the original material of *P canadensis* Moench, I visited during the summer 1956 the Wilhelmshöhe-park and the Natural History Museum at Kassel.

In the Wilhelmshöhe-park unfortunately we could not find a single poplar older than 100 years; therefore it is obvious the original trees described by Moench do not exist any longer. The Museum was for the greater part destroyed by bombs during World War II, and all records, including Moench's herbarium, were burned. Fortunately I found in the nearly restored Museum an old xylothec [1]) made by C Schildbach, and of this work a detailed description exists (SCHILDBACH, 1788). The periodical in which this description was published is also very rare, but by the kind co-operation of the retired Director of the botanical garden at Kassel, now in charge of the restauration of the botanical section of the Museum, Mr. H. Schulz, I obtained from the famous government-library in Vienna a fotocopy of the article.

This article says among other things:

„Meine Holzbibliothek ist eine Sammlung von mehrentheils Deutschen Hölzern, die sich umweit Cassel bey dem Fürstlichen Lustschloss Weissenstein in den neuen Anlagen befinden".

MOENCH writes in 1785 (pag. III) that the oldest trees in the park were not more than 16 years, and from two lists compiled by Prof. Böttinger, which lists I unfortunately could not find, it is possible to conclude that already in those years several trees were dead and had been replaced by others. This is in accordance with the information given by Schildbach in 1788, that he took his material from the new plantations. If we see further that the order of the wooden boxes in the xylothec is exactly the same as in Moench's publication, we may venture to say that the specimens preserved in this xylothec were collected from the trees described by Moench.

Schildbach's list records on p. 326: "No. 188, *Populus canadensis*". The contents of this small box were luckily totally intact and in good condition; it shows a branchlet with leaves and a second one with fruits; the soaked leaves are reproduced in fig. 1. The form of these leaves is similar to that of the leaves of *P. deltoides*, but I could not find a single gland on them; the somewhat cuneate base reminds one of *P. nigra* L. Anyway it is evident that the characters of the material in box 188 agree with the Moench's description; furthermore I found that the contents of the xylothec boxes representing other poplar-species also agreed with Moench's descriptions. Therefore I am convinced that we may safely accept the contents of box 188 of Schildbach's xylothec as neotype of *P. canadensis* Moench.

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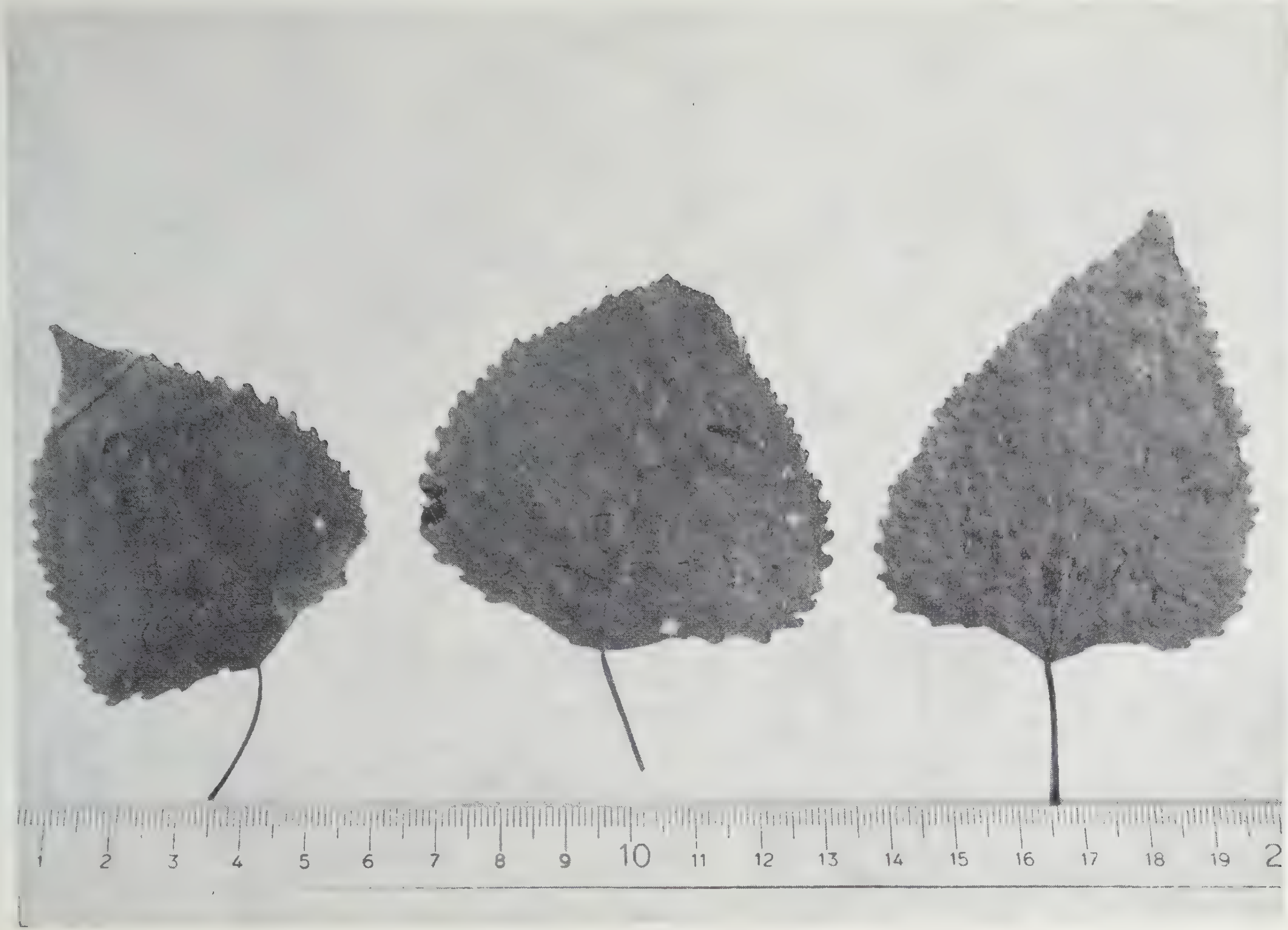
[1] A xylothec is a collection of small boxes in book-shape, each box made of the wood of a particular tree, and containing herbarium material as complete as possible of this very tree, mostly accompanied by special information of the wood concerned, and often also by herbarium material of fungi, lichens and mosses found on the trees at the time it was collected. Xylothecs are scarse, only a few existing in the whole world. They nearly all originated at the end of the 18th century.



Populus canadensis Moench, 3 leaves from box 188 of Schildbach's xylothec.

Which clone it presents is not absolutely certain, but the leafshape and the female character suggest that it may be cv. "regenerata".

2. THE NAME P. EURAMERICANA GUINIER

This name was validly published and is accompanied by a latin diagnosis; it is very positively stated that the name is intended to cover all segregates of the hybrid *P. deltoides* x *P. nigra*. As there are older names for this group of segregates, it is a superfluous one. Before 1950 certain poplar clones had already been named and described as belonging to this hybrid, e.g. *P. robusta* SCHNEIDER (1904). Furthermore the citation of the author's name is incorrect: we find on page 5: *P. euramericana* (Dode) Guinier, but DODE (1933) writes "Peupliers euramericains" and the citation of Dode's name within brackets is therefore not justified.

It is regrettable that an International Committee which cares for the registration of poplars, goes on to use an illegitimate name for a poplar group that is widely planted, and refuses to observe the international rules laid down in the Code of botanical nomenclature.

However we may hope that this Committee will admit its error, and that it will reject the name *P. euramericana* Guinier in favour of *P. canadensis* Moench.

The naming of the clones or populations of this hybrid follows the International Code for nomenclature and registration of cultivated plants, the most important clone names being:

P. canadensis Moench cv. **„Marilandica"** (Bosc) [1]
P. marilandica Bosc ex Poiret, Enc. suppl. 4 (1816) 378.
P. canadensis Moench cv. **„Serotina"** (Hartig)
P. serotina Hartig in Naturgeschichte der forstlichen Kulturpflanzen Deutschlands, 1852, 437.
P. canadensis Moench cv. **„Robusta"** (SimonLouis)
P. robusta SimonLouis ex Schneider, Ill. Handb. Laubholzkunde, 1 (1904), 11.
P. canadensis Moench cv. **„Gelrica"** (Houtzagers)
P. gelrica Houtzagers, Het geslacht Populus, 1937, 141.

SUMMARY

1. The name *P. canadensis* Moench is the correct one for the hybrid *P. deltoides* x *P. nigra*.
2. The neotype of *P. canadensis* Moench is preserved in the Schildbach's xylothec under no.: 188. This xylothec is kept in the Natural History Museum at Kassel (Germany).
3. The name *P. euramericana* Guinier is superfluous and therefore illegitimate.

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[1] The cultivar epithet does not form a technical nomenclatural combination with the generic, specific or varietal name to which it is attached (see Art. C 19, Note 1); if the name of the raiser, introducer or describer is cited, this remains the same even when the name preceding the cultivar-name is changed (see Art. C 19, Note 2). This name is then cited in brackets.

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PLANT-MIGRATION STUDIES NEAR THE FORMER ISLAND OF URK IN THE NETHERLANDS

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INTRODUCTION

Reclaimed in 1941 and 1942, the North-Eastern polder [1]) is the second reclamation district in the former Zuydersea, now being called IJssellake. Its formation added 48,000 ha of land to the Netherlands. The virgin soil of this polder mainly consists of sand and silty clay-loam and lies at about 0.5–4.0 m under mean sea-level. Upon these soils within just a few years an almost closed vegetation developed, in which predominated *Phragmites communis* Trin., *Scirpus maritimus* L., *Aster tripolium* L.,*Senecio tubicaulis* Mansf., *Polygonum nodosum* Pers., *Atriplex hastata* L., *Chenopodium rubrum* L. and species of the genus *Bidens*; all these species are pioneers on fertile, waterlogged unaerated soils. Locally saline soils occurred and on these *Puccinellia distans* Parl., *P. retroflexa* Holmb. and *Spergularia salina* J. et C. Presl flourished. With the exception of part of the seeds of *Phragmites*, *Aster* and *Senecio*, in this area propagules of all species mentioned above were distributed almost exclusively by water of the IJssellake from the coastal region, the mouths of the rivers or the islands of Urk and Schokland (Fig. 1). Prior to the reclamation of the polder propagules became deposited on the bottom of the lake, the submerged future polder. After being dispersed by wind into the IJssellake even a considerable number of seeds of typically wind-dispersed species was carried along further into the area of the future polder by means of water transport. Vegetation of *Aster* mainly arose from achenes sown by man during the first two years after reclamation and collected on salt marsh lands in the northern part of the Netherlands (FEEKES and BAKKER, 1954).

For the ecesis of the species mentioned above it is very important that their seeds, if kept under water, can maintain their germinative capacity for at least one year. Transport of rhizomes of *Phragmites* and *Scirpus* by water of the IJssellake occurred but very rarely and consequently in this publication this way of dispersal will not be considered.

Owing to the predominating influence of the water of the IJssellake as dispersing agent for the predominating species and also due to the great competitive power of these species, the North-Eastern polder as a whole proved to be a less favourable object for plant-migration studies than was initially expected (FEEKES and BAKKER,1954). As a consequence of the competitive power within a couple of years an almost closed vegetation arose and species dispersed by other agents than water hardly got any opportunity to become established. However, in the extreme western part of the reclamation district, in the vicinity of the former island of Urk an area of about 800 ha, differed botanically and pedologically considerably from the main part of the polder. In this publication this area will be called Land of Urk. Pedologically it is characterized by an oftentimes very complex mixture of soil types and a higher location (at 0.5–2.5 m under mean sea-level) than the remaining part of the polder (at 2.0–4.0 m under mean sea-level). Its botanical pecularities were a rather open type of vegetation, very rich in species, and a large variation in plantcover over small distances, parallelled by sudden changes in soil conditions. From 1941, the year of reclamation, to 1951, the year of cultivation, this natural vegetation could develop undisturbedly. The isolated location of the district, the great variation in edaphic factors and the rather general absence of a closed vegetation with only few predominating species made this area extremely well suited to plant-migration studies, the results of which will be discussed in the following paragraphs.

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[1]) a "polder" is an area, reclaimed from the sea and protected against flooding by dikes.

THE PEDOGENESIS OF THE LAND OF URK

The geologically oldest deposits present at the surface are so-called pro-morainal sands, layed down prior to or simultaneously with Riss-morainal boulder clay. They were subject to a strong pushing influence of the icecaps, which deposited on top of them a cover of boulder clay, now lying at or very close to the surface. In the latter case it is covered by a thin layer of still younger deposits. During the Zuydersea period (1500–1932) a shallow water layer inundated the soils and they suffered heavily from wave action, resulting in the actual local presence at the surface of pure boulder clay.

A peat profile forms at present the topsoil in large areas east as well as south of the boulder clay region. Probably prior to 1000 A.D. fresh-water clay became deposited upon this peat. In the Zuydersea period again the sea encroached upon the area and previously off-shore lands were flooded, unless protected against this fate like on the island of Urk.

Another consequence of the rise in sea-level was the distribution of much sandy material by water. Originally this material was lying against or upon the hill of boulder clay or elsewhere it came to the surface through the eroding action of waves. Nowadays these Urk-sand deposits can be found in the peat area and all through the vicinity. Also the two sandy ridges, bordering the low-lying clay area of the island of Urk, are composed of this material as well as the "Tail of Urk". This Tail was a bank of very coarse gravelly and sandy material, projecting in north-eastern direction into the Zuydersea and after the reclamation arising in the landscape as a ridge. The subsoil of this bank was formed by fresh-water clay. In 1952 the material of the Tail was removed and utilized for building purposes.

Boulder clay, peat, Urk-sand and fresh-water clay form in a broad outline the pattern of soil types offered to the vegetation as habitat. For purposes of soil improvement during the construction period of the polder dikes large amounts of soil were deposited on the lake floor. This material originated from canals dredged out under water and is mainly of a light silty clay-loam character; the thickness of the layer is variable.

The natural vegetation of the Land of Urk

Based upon the soil characteristics mentioned in the previous chapter the authors distinguish the following six types of habitat:

1. Urk-sand and light silty clay-loam (dumped soil,) with a maximal thickness of 35 cm;
2. fresh-water clay and light silty clay-loam (dumped soil), in a layer heavier than 35 cm;
3. boulder clay;
4. Tail of Urk;
5. saline soils;
6. peat district.

Many times in types 2, 3 and 6 the soil type giving its name to the habitat does not occur at the surface but is covered by a thin layer of overlying sand. Frequently, however, this layer is so shallow or the influence of the subsoil upon the physical and/or chemical character of the profile so great that the pedological characterization of the habitat offers a good starting point to an ecological discussion.

During the first years after reclamation vegetation remained poor in species. Although usually in a little vital form, only those species occurred which were also predominating in the remainder of the North-Eastern polder. Consequently vegetation stayed open; particularly conspicuous were *Puccinellia*-species, propagules of which were supplied by the water of the IJssellake. Even in 1951 hardly any plant community could be distinguished although particularly after 1945 the total number of species present increased considerably. For a great part propagules of these species were wind-borne, a phenomenon to be returned to later on. First will be given a rough description of the vegetation of the 6 habitats as present during the years 1948–1950.

1. *Urk-sand and dumped soil with a maximum thickness of 35 cm*

In this region the all-predominating environmental factor was the water-economy. An almost completely closed vegetation could develop at some scattered low-lying spots at which the supply of water was guaranteed during the entire vegetation period. Usually, however, the habitat was less favourable due to the bad water-retaining capacity of the soil and the depth of the soil-water table. Particularly during the dry early summer periods vegetation here was very sparse and not before the more rainy summer months most plants came to flower. Consequently in this area the following seasonal vegetation aspects could be distinguished:

winter season: development of mosses and rosettes of winter annuals and perennials;

spring: development of mosses and flowering of some winter annuals (*Cerastium semidecandrum* L.) and perennials, *Taraxacum spec. div.*;
early summer: rather "dry" vegetation, flowering of some winter annuals, e.g. *Erigeron acer* L., *Bromus mollis* L.;
summer and late summer: flowering of many plants which overwinter with a rosette, e.g. *Epilobium spec. div.*, yellow flowering *Compositae.*

In this area species which usually occur under quite dry environmental conditions, strongly predominated. Higher plants covered 40–80 % of the soil surface.

2. *Fresh-water clay and dumped soil with a layer thicker than 35 cm*

In early spring these habitats were flooded for a shorter or longer period of time or they suffered from very high watertables. Many species preferring moist habitats occurred. The main part of the soil surface was occupied by species able to propagate very actively by means of subterraneous organs, e.g. *Phragmites communis* Trin., *Scirpus maritimus* L., *Tussilago farfara* L., *Cirsium arvense* Scop. The vegetation covered the area for about 80–100 %.

3. *Boulder clay*

On boulder clay like on other compact soils many plants suffer unsurpassable difficulties owing to the great resistance offered to the development of the root systems and due to the large swelling and shrinking characteristics of the soil material. Even in 1950 vegetation was still very sparse; the part of the soil covered by higher plants did not amount to more than 5–15 %, while 10–20 % was occupied by mosses.

As on peat soils the presence on the boulder clay of a shallow sandy layer appeared to promote the establishment of plants. Due to the imperviousness of the subjacent boulder clay such a sandy layer could keep its humidity rather long. Moreover, aeration of the sand was high and mechanical resistance very little. The major part of the species present were winter annuals, common on quite dry habitats, e.g. *Erigeron acer* L., *E. canadensis* L., *Crepis capillaris* Wallr.

4. *The Tail of Urk*

On the Tail the coarseness of the material increased with increasing elevation. However, even at the top of the ridge in early spring the phreatic level was not very low owing to the presence of the clayey subsoil. The striking coarseness of the topsoil permitted development of those species only, which are drought resistent or have during the wet season such a rapid root development that this feature enables them to reach the watertable very rapidly. Part of the species belonging to the latter type succumbed in the dry early-summer period before ever having flowered.

On top of the Tail the cover of higher plants did not amount to more than 5 % of the total surface; mosses took in 10–30 %. The whole year through the xerophyte *Sedum acre* L. determined the aspect.

5. *Saline soils*

The area east and south-east of the island of Urk has received the name heterogeneous complex, indicating that patches of peat, sandy areas, fields of fresh-water clay and other young marine sediments are intermingled in a very irregular fashion. Also north-west of Urk and south of the boulder clay area regions of this character can be found. Locally environmental conditions occurred which could only be met by halophytes.

6. *Peat area*

Botanically the peat area was characterized by a very sparse vegetation (cover 0–20 %) and by the presence of narrow but rather densely vegetated bands, formed on clayey or mixed sand-clayey ridges, resulting from human activities in former ages. Compared to the other sparse vegetations on the boulder clay and the Tail, on account of the absence of even the slightest cover of mosses the peat area could be called the poorest vegetated part of the Land of Urk.

The peat area suffered from a very bad water-regime, owing to its location between the former island of Urk, the dike of the North-Eastern polder and the boulder clay region. Consequently chlorine, concentrated in the peat by diffusion during the saline Zuydersea period, could only be partly leached out. Through evaporation during summer months particularly at the surface layer of the peat locally very high salt contents could be reached.

In addition to these saline spots (salinity expressed as content in NaCl) the peat was characterized by a very high acidity. Formed in fresh water and very poor in mineral elements, after reclamation the acidifying influence of oxidative processes in the topsoil could not be neutralized. This resulted in the formation of hydrochloric acid because a large amount of chlorine ions occurred in the soil moisture in addition to sulfuric acid formed through oxidation of FeS.

On the saline peat halophytes rarely occurred, probably due to the low pH. All Dutch halophytes are base-frequent and of non-halophytic acid-frequent species only *Holcus lanatus* L. predominated.

THE MIGRATION OF PLANTS TO THE LAND OF URK

The ecesis of a plant at a specific habitat is the result of the action of a great number of factors, which can be separated into the two following groups:

1. the environmental factors;
2. the life-cycle of the plant.

As to the environmental factors, in a discussion of the migration of a plant species particularly the factor called accessibility (*sensu* HEIMANS, 1954) is of importance. Of the life-cycle characteristics the dispersal type has to be stressed.

Considering the accessibility of the Land of Urk two periods have to be clearly distinguished, viz. the period prior to and the period after the reclamation of the North-Eastern polder. Prior to reclamation propagules became deposited upon the lake bottom and after emergence of the land establishment of plants was possible. After reclamation only those plants could ecese which have propagules able to pass the distance between the area and the island of Urk or the much larger distance to the island of Schokland or to the still existing or former shore of the IJssellake (Fig. 1).

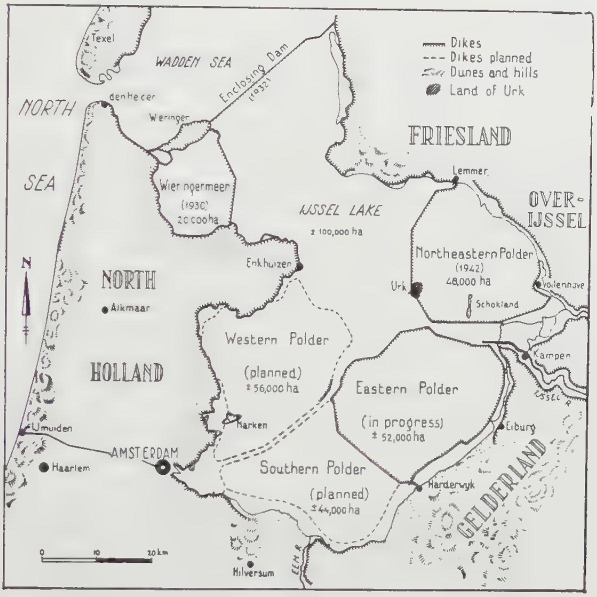

Fig. 1. Sketch-map of the Zuydersea reclamation works and adjacent areas.

In distinguishing several dispersal types use has been made of the principles followed by FEEKES (1936) and WESTHOFF (1947). As criterion for the distinction of dispersal types these authors used the effectiveness of the action of the distributing agent upon the propagule measured by the distance between mother plant and the spot that can be reached by the propagule. In our discussion the classification of Westhoff is followed (Table 1), differing only in minor details from the one used by Feekes.

WESTHOFF (1947) subclassifies these dispersal types respectively into euchorous or migration types (propagules of which can be dispersed over long distances) and dyschorous types where this is not the case. Of the types mentioned in Table 1, type A, *a*, H, Z and M are considered to be euchorous, type a, h and z dyschorous by Westhoff. From Table 2 it appears, that in the pioneer vegetation of the Land of Urk euchorous types were stronger represented than in the older vegetation of the islands of Urk and of Schokland.

TABLE 1

Dispersal-types according to Westhoff (1947)

A = anemochorous; propagules dispersed by wind over some to many kilometres.
a = anemochorous; propagules dispersed by wind over not more than some hundred metres to about one kilometre.
a = anemochorous; propagules dispersed by wind over at the most some tens of metres.
H = hydatochorous; propagules dispersed by water, remain floating for some weeks to years.
h = hydatochorous; propagules dispersed by water, remain floating for some hours to days.
Z = zoochorous over great distances, i.e. endo- or epizoochorous due to dispersal by birds.
z = locally zoochorous, dispersal by mammals, ants, etc.
M = anthropochorous, propagules dispersed by man.

TABLE 2

Dispersal spectra of the vegetations of the islands of Urk and of Schokland and of the Land of Urk. The occurrence of polychory is taken into consideration.

	Urk, 1941	Schokland, 1941	Land of Urk, 1942–1951
Total area	80 ha	119 ha	800 ha
Number of species Dispersal types	165	196	182
A	20.6 %	23.0 %	40.2 %
a	23.0 %	25.5 %	26.9 %
a	27.8 %	28.6 %	17.0 %
H	17.5 %	19.4 %	18.6 %
h	45.4 %	57.6 %	53.8 %
Z	28.4 %	25.5 %	29.1 %
z	30.9 %	35.7 %	38.4 %
M	28.7 %	20.4 %	14.3 %
Sum of euchorous types	118.2 %	113.8 %	129.1 %

Migration proper was strongly influenced by all factors affecting germination of seeds. Due to this influence it is not known which propagules reached the area, neither in what degree they germinated. We only know which plants, whose propagules reached the area, passed through the entire ecesis stage, i.e. after the migration stage they came to germinate, development and reproduction.

It did not appear to be possible to follow along experimental lines the behaviour of different dispersal types in relation to the very remote location of the area, in other words the interaction between remote location and dispersal type. We could only proceed statistically in comparing the dispersal spectrum of the vegetation of the Land of Urk with the dispersal spectrum of the vegetation of the neighbouring island of Urk, which for our area will have been a source of propagules, and also of the island of Schokland. For this purpose species inventories of Urk and Schokland, taken by Feekes (1942) in 1941 shortly before the reclamation of the Land of Urk, were at our disposal ²). Moreover we followed whether or not species present in the Land of Urk could originate from the mainland between Lemmer and Kampen, thoroughly floristically investigated during the years from 1929 to 1941 (FEEKES and BAKKER, 1954). Supply of propagules from habitats in the province of North-Holland could not be considered, because accurate species inventories of this region were not available. Almost exclusively supply by wind or by birds comes into consideration, considering the water barrier between the districts.

Until 1932 the island of Urk was surrounded by the brackish water of the Zuydersea, and this became expressed in the halophilous vegetation. After the enclosure in 1932 the tidal effect disappeared and the IJssellake freshened due to the continued supply of fresh water by several rivers and drainage canals. Since ages people have been living on this island and this has found its expression in the vegetation.

At about 5.5 km from the main coast, around the island of Schokland (about 119 ha) the water was less salt than in the neighbourhood of Urk owing to the influence exerted by estuaries. Yet during the brackish period a number of salttolerant species occurred on Schokland. Only 26 ha were covered with grassland, 52 ha were *Phragmites*-vegetation while along the western border not less than 41 ha were taken in by shallow pools. From about 1860 to 1941 human habitation and other presence of people or cattle on the island was negligible and consequently compared to Urk the influence of man upon the plant-cover remained very small (FEEKES, 1942). This is also demonstrated in the dispersal spectra of Table 2.

It has to be remarked that in the calculation of percentages of dispersal types represented most species were placed under more than one dispersal type (polychory), making the sum total of percentages in the different columns of Tables 2, 3, 4 and 6 surpassing considerably the figure 100. E.g., *Phragmites communis* Trin. was classified under type A, h and z, and *Trifolium repens* L. under H, Z and M.

RIDLEY (1930) and MOLINIER and MÜLLER (1938) pointed out that wind is the most important agent in the migration of species to open vegetations, while OSTERWALD (ULBRICH, 1928) demonstrated this phenomenon very clearly in the establishment of pioneer vegetations in a large sand-pit near Berlin and SALISBURY (1954) for the flora occurring on World War II bomb-sites in London. In agreement with these observations are the data of Table 2, from which we can conclude the tremendous importance of the wind factor for the formation of the pioneer vegetation of the Land of Urk, compared with the old established and almost closed vegetations of the islands of Urk and of Schokland. From Table 3 we can also draw the conclusion that the majority of the species of type A present in our area could not originate from the island Urk (although the Land of Urk was so closely adjacent to it) or from Schokland but came from the mainland. Moreover, only

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²) The list of species could not be included in this publication. However the authors are willing to send interested persons a mimeographed list with indication of the dispersal types of all species found on and near Urk and on Schokland.

17.8 % of type A could have been dispersed over large distances by other agents than wind. Of these 17.8 % still 76.9 % was present on the island of Urk, making it highly probable that most species belonging to this type were borne by wind from Schokland, from the mainland between Lemmer and Kampen or from still further lying dispersal nuclei (Table 4). Only five species occurring in the Land of Urk were never found on the mainland between Lemmer and Kampen; of these 5 species 4 belong to type A (Table 5).

It is of no use to make a sub-classification of type A considering the rather small establishment of species in the Land of Urk. Mention can be made though of the occurrence of a great number of *Compositae*, "presenting" their fruits to the wind like *Taraxacum* does with a well-developed pappus.

In the Land of Urk, however, type *a* did not come more to the fore than on the two islands (Table 2); the majority of the representatives of this type also occurred on Urk and they may have originated from this island (Table 3). The dyschorous type a, however, was in the Land of Urk considerably less represented than on the two islands (Table 2). Probably thanks to the adjacent location of Urk this type was still able to attain a percentage of 17.0; the majority of the species was represented on Urk (Table 3) and those that were not did also belong to the euchorous types H, Z or M.

In the Land of Urk supply of propagules by lake water played a less predominating part than elsewhere in the North-Eastern polder. During the first few years after reclamation not one fourth of the total number of species present later on became established here. Probably this was due to the extreme drought conditions during summer, still permitting establishment of hydatochorous plants but not allowing development of a dense vegetation. That is to say, in the Land of Urk almost all species, predominating in the major part of the North-Eastern polder, became established immediately after reclamation. The percentage of typical hydatochorous plants (type H) did not differ noteworthy from that on the two islands (Table 2), so that this dispersal type is not characteristic for the pioneer vegetation under discussion. Moreover in 1941 81.1 % of the representatives of this type occurred on Urk and consequently a fast supply of propagules from far-removed dissemination nuclei cannot be proved, the more so as for 87.5 % of the type H species of the Land of Urk transport over large distances by other agents than water was possible (Table 4). Type h strongly predominated on the two islands and in the Land of Urk (Table 2) because many representatives of type A are also classified under "minor hydatochorous plants". Very probably, however, in the Land of Urk the majority among the h-group was not supplied by water of the IJssellake since many representatives of this type did not become established until several years after reclamation. It is striking that on the island of Schokland the percentage of species belonging to type h was higher than in the Land of Urk, although in the first region type A was considerably less represented than in the latter. However, also on Schokland many species occurred for which type h is one of the most important ways of dispersal. Probably this was a result of its location at a rather short distance from the coast just in front of some rivermouths.

In the three regions under consideration quite a few typically zoochorous species (type Z) were found (Table 2). Yearly use of the islands as resting-places by many migratory birds may explain the quite frequent occurrence of type Z (TEN KATE *c.s.*, 1931, 1933). Feeding-experiments with ducks (EIKELBOOM, 1941, 1942) and with starlings (DE VRIES, 1939), as well as the results of investigation of crop and stomach contents carried out with ducks clearly demonstrate that seeds of many plant species can pass through the digestive tract of above mentioned birds without loosing their germinative capacity. In ducks digestion may take some 4–7 hours; within this time ducks can transport seeds over some hundreds of kilometres (EIKELBOOM, 1942). Epizoic dispersal may be very effective too when fruits and seeds stick with muddy soil to the legs or feathers of birds (RIDLEY, 1930). Particularly small fruits and seeds, and fruits and seeds carrying a pappus or wings come into consideration for this transport. However, it cannot

TABLE 3

Occurrence on the islands of Urk and of Schokland and on the mainland between Lemmer and Kampen of the 182 species represented in the Land of Urk. Species grouped according to dispersal type and polychory taken into consideration.

	Urk, 1941	Schokland, 1941	Mainland between Lemmer and Kampen, 1929–1941
Number of species	102	110	177
Dispersal types			
A	39.7 %	47.9 %	94.6 %
a	75.0 %	69.4 %	97.6 %
a	66.7 %	72.7 %	100 %
H	81.1 %	72.5 %	100 %
h	60.0 %	38.9 %	96.6 %
Z	71.1 %	75.0 %	98.1 %
z	52.1 %	63.5 %	97.3 %
M	65.4 %	65.4 %	100 %

TABLE 4

Percentages of different euchorous dispersal types, present in the Land of Urk, belonging to more than one euchorous dispersal type and occurrence of these subgroups on the island of Urk in 1941.

Euchorous dispersal types	Belonging to more than one euchorous dispersal type	Occurrence on Urk in 1941
A	17.8 %	76.9 %
a	44.9 %	40.6 %
H	87.5 %	85.9 %
Z	76.9 %	75.0 %
M	38.6 %	90.0 %

always be ascertained whether transportation occurred epi- of endozoïcally, because some species can be distributed either way.

During fall and winter months the Land of Urk was covered by vast pools and continuously visited by water-fowl making supply of propagules by birds very probable. Presumably thanks to the favourable biotope for water-fowl and due to the proximity of the island of Urk (where 71.1 % of the typically zoochorous species present in the Land of Urk occurred, Table 3) about 1951 within a short period of time the percentage of type Z species increased tremendously. Although being very probable yet it cannot be said with certainty that zoochory has been of great importance in the Land of Urk because in this area 76.9 % of type Z species belonged to other euchorous dispersal types as well (Table 4).

Not including the salt-tolerant *Carex extensa* Good. all typically zoochorous species present in the Land of Urk were also found on the mainland between Lemmer and Kampen (Tables 3 and 5). The nearest growth sites of *Carex extensa* are at about 70 km from the island of Urk at the saline beaches of the Wadden Islands and supply of propagules by migratory birds is highly probable.

In the Land of Urk the percentage of locally zoochorous species (type z) was somewhat higher than on the two islands because several typically anemochorous species (type A) were also recorded under type z. This explains why only 52.1 % of type z present in the Land of Urk occurred on the island of Urk.

In the Land of Urk anthropochorous species (type M) played only a minor part. Yet 14.3 % of the species present belonged to this type, undoubtedly owing to the proximity of the island where 65.4 % of the species occurred. Another factor responsible for the rather high percentage of type M species is the sowing in 1947 on the Urk-sand of some small trial plots with pasture seed mixtures.

Species belonging to type A had a more conspicuous representation in the usually open vegetation of the Land of Urk than in the completely or almost completely closed vegetation of the two islands (Table 2). From this we see that a dispersal spectrum does not include all species which migrated to an area but only those species able to establish themselves after migration thanks to a suitable environment. Apparently in open vegetations conditions are more favourable to the establishment of representatives of type A. Usually pioneers do not form closed vegetations and consequently type A species will play an important part in them.

TABLE 5

Species present in the Land of Urk and not occurring on the islands of Urk and of Schokland and neither on the mainland between Lemmer and Kampen.

Species	Dispersal types
Carex extensa Good.	*a*, h, Z
Epilobium adenocaulon Hausskn.	A, z
Epilobium lanceolatum Seb. et Mauri	A, z
Gnaphalium luteo-album L.	A, h
Hieracium caespitosum Dum.	A, h

The vegetations on the six types of habitat mentioned previously developed almost simultaneously, only at the relatively elevated Tail some months earlier than elsewhere. There was not much difference either in location of the dispersal nuclei Urk, Schokland and the mainland between Lemmer and Kampen. Nevertheless it was of great importance that the six habitats differed greatly in extension, a factor which might have been of influence upon the supply of very rare migrants. This does not take away, however, that based upon the similarity in location and period after emergence some conclusions can be drawn from a comparison of the dispersal spectra of the six habitats. The more so as the smallest region carried the greatest number of species per unit of area and the largest as well as the smallest region were taken in by open vegetations (Table 6).

TABLE 6

Dispersal spectra of the vegetation of six habitats in the Land of Urk, polychory taken into consideration.

Habitat	Urk-sand and dumped soil < 35 cm	Fresh-water clay and dumped soil > 35 cm	Boulder clay	The Tail	Saline soils	Peat
Total area	350 ha	200 ha	50 ha	25 ha	50 ha	125 ha
% cover by vegetation	40–80 %	80–100 %	5–15 %	5–15 %	50–70 %	0–20 %
Number of species	170	74	63	76	40	47
Dispersal types						
A	41.7 %	29.7 %	50.8 %	50.0 %	30.0 %	44.7 %
a	27.1 %	32.4 %	29.0 %	23.6 %	35.0 %	27.6 %
a	17.1 %	22.9 %	14.3 %	14.4 %	20.0 %	23.4 %
H	17.1 %	31.1 %	19.0 %	18.4 %	55.0 %	31.9 %
h	53.5 %	54.1 %	60.3 %	53.9 %	42.5 %	53.2 %
Z	28.2 %	40.5 %	25.4 %	23.7 %	62.5 %	40.4 %
z	37.6 %	37.8 %	47.6 %	40.8 %	22.5 %	42.5 %
M	14.6 %	12.2 %	15.8 %	13.2 %	2.5 %	8.5 %

It follows from Table 6 that not including the saline area, in all open vegetations type A was the most occurring euchorous dispersal type. At the saline habitats soil conditions had a very selective influence and ecesis of plants mainly occurred by salt-tolerant species, which are in the IJssellake region for a considerable part of typically hydatochorous and zoochorous character. Particularly in the very sparse vegetation on the boulder clay type A predominated, and also on the Tail and in lesser extent on the peat soils. Great humidity and locally occurring saline conditions caused that also on the peat a rather high percentage of typically hydato- and zoochorous species occurred. Type A also was of major importance in the quite dense vegetation of the Urk-sand and dumped soil regions. In the dense vegetation of the moist fresh-water clay area, however, typical anemochorous species decreased in importance, presumably due to the rapid establishment of representatives of types H and Z. On the fresh-water clay only a limited number of species predominated, a phenomenon also expressed in the small number of species per unit of area.

Conclusions

From a comparison of the dispersal spectra of the Land of Urk and the islands of Urk and of Schokland it appears that in open vegetations typical anemochorous plants are predominant among the euchorous dispersal types, and we come to the same conclusion when comparing such spectra of six habitats, offering diverse environmental conditions. Pioneer vegetations usually not being closed, the most important agent in the supply of propagules will be mainly wind. Based upon our own investigations in the Land of Urk and upon experimental results and observations of Osterwald (Ulbrich, 1928) and Salisbury (1954) we conclude, that type A characteristics are important features in pioneers, at least in Western Europe. It could not be experimentally determined whether the open character of the vegetation plays a part during the migration phase of type A representatives, or that a partly vegetated habitat is of importance during the process of ecesis. It is very likely, however, that dense vegetations (particularly high forest) may hamper penetration of propagules borne by wind. Under very extreme edaphic conditions (in our case salinity) even in open vegetations typical anemochorous species were represented in a very low percentage. Salt-tolerant species of dispersal type A never occurred in great amount in the Zuydersea region and consequently their migration to the Land of Urk was only of limited importance. The investigations reported on here prove that environment has a great influence upon the composition of dispersal spectra, in other words in addition to edaphological factors accessibility can be of decisive importance.

SUMMARY

1. In the neighbourhood of the former island of Urk within the North-Eastern polder an area of about 800 ha, called Land of Urk, is distinguished from the remainder of the reclamation district by very peculiar soil conditions. Compared to plant establishment elsewhere in the polder also the development of a natural vegetation showed great differences. From 1941 until 1951, the development of natural vegetation proceeded almost undisturbedly.

2. Based upon differences in soil conditions in the Land of Urk six habitats were distinguished. Differences in soil conditions were strikingly parallelled by variation in vegetation.

3. The Land of Urk was extremely well suited to studies in the field of dispersal-biology. In our investigations use was made of dispersal types distinguished by Westhoff (1947), based upon the degree of interaction between the propagules and the various dispersal agents (Table 1). Only dispersal of fruits and seeds has been of importance.

4. From the euchorous dispersal types represented in the Land of Urk the highest percentage was taken in by species propagules of which can be wind-borne over many km (type A). However, in the dispersal spectra of the closed or almost closed vegetations of the adjacent islands of Urk and Schokland, type A was represented in a considerably smaller degree (Table 2).

5. In 1941 among the representatives of type A in the Land of Urk the major part did not occur on the island, whereas the other types for the most part were

found on Urk. In all probability the most important source of propagules of type A has been the island of Schokland and/or the mainland between Lemmer and Kampen (Fig. 1, Tables 3, 4 and 5).

6. A comparison of the dispersal spectra of the six types of habitat distinguished demonstrated that, excluding saline soils, in open vegetations type A was the most dominant euchorous dispersal type. The accessibility of a habitat appears to be of great influence upon the composition of the dispersal spectrum.

7. The authors propose the thesis that at least in Western Europe type A is the dispersal type par excellence for open vegetations and the characteristics of this type are important features of pioneers, pioneer vegetations usually being open.

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TARAXACUM SECTIO OBLIQUA DT. EN SECTIO ERYTHROSPERMA DT. EM. LB. IN NEDERLAND

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Deze studie is te beschouwen als een vervolg op „Het Geslacht Taraxacum in Nederland I", Nederlandsch Kruidkundig Archief 49 (1939), in den vervolge aangeduid als NKA l.c.

In 1948 maakte ik met Dr G. E. Haglund een afspraak de Nederlandse vormen der *Erythrosperma* gezamelijk te revideren; zijn ziekte en daarna zijn dood beletten de uitvoering van dat plan. Zijn bezoek aan Nederland in 1949 en zijn revisie van een klein deel van het materiaal gedenk ik met dankbaarheid.

Meer dan vroeger ondervond ik hulp bij het verzamelen, hetgeen in het bijzonder de geografische kennis der soorten in Nederland ten goede is gekomen. Het land is vrijwel doorkruist; voor de *Erythrosperma* en *Obliqua* is één leemte overgebleven: materiaal uit de duinen van Goeree en Schouwen.

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De afbeeldingen zijn door mijn vrouw getekend.

SECTIO OBLIQUA DT.

1. **Taraxacum obliquum** (Fries) Dt. 1905, Bot. Not. — *T. officinale* var. *obliquum* Fries 1814.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 27, pl. XI; v. S., NKA l.c. fig. 1.

Exsiccata: Dahlstedt I. 1 (s.n. *T. platyglossi*).

Areaal: westelijk Estland, Z. Zweden en Gotland, Z. Noorwegen, Denemarken en Bornholm, kustzône van N. Duitsland en Nederland.

Nederland (kaart I a): Waddendistrict en Duindistrict zuidwaarts tot Voorne, welk eiland de zuidelijkste vindplaats in het areaal is. Aanvullingen op de gegevens uit NKA l.c., alwaar ook een uitvoerige beschrijving van de soort gegeven is:

Schiermonnikoog! *v. S.*; Terschelling, Landrummerheide *W.* (h); Texel, de Koog en omgeving *Hagl.* & *v. S.* (h); Huisduinen en Falga *B.* & *v. S.* (h); Castricum, Heemskerkerduin en Egmond, alle *v. S.* (h); Zandvoort-Bloemendaal *J. Prins* (h. Go.); Vogelenzang *de J.* (h); Noordwijk-Katwijk *de J.* (h) & *v. S.*; ten Z. van Katwijk *Alston* (h); Rockanje, op verschillende plaatsen *v. S.* (h).

T. platyglossum Raunkiaer, in NKA l.c. vermeld, is voor Nederland onzeker; de door Christiansen als *T. platyglossum* gedetermineerde planten van Scheveningen-Wassenaar zijn vermoedelijk *T. obliquum* en die van de Scheveningse Boschjes behoren tot *T. tortilobum*. Het areaal van *T. platyglossum* en *T. obliquum* is overigens vrijwel gelijk.

SECTIO ERYTHROSPERMA DT. EM. LB.

SUBSECTIO DISSIMILIA DT. (pro sect.).

2. **Taraxacum tortilobum** Florstroem 1941, Acta Soc. Fauna Fl. Fenn. 39.4.

Icones: Dt., Kungl. Sv. Vet. Ak. Handl. 3.6.3 (1928) fig. 2; v. S., NKA l.c. fig. 3; v. S., Bull. Rijkspl. t. Brussel 26 (1956) fig. 67.

Areaal (kaart IVa): Nederland, België, W. Duitsland, N. en O. Frankrijk tot in het Rhônegebied en Corsica, Zwitserland; ten slotte sporadisch en wel steeds aangevoerd in het gebied om de Oostzee.

Deze soort, in NKA l.c. voor Nederland aangegeven en beschreven, is onder de *Erythrosperma* in Nederland de enig algemene soort met strokleurige vruchten. Zij is algemeen op licht grazige zandgrond, vooral in de duinstreek, maar zeldzaam in het hart van het Drentse en van het Kempische district; elders in het land vindt men haar met zand aangevoerd langs wegen en dijken en op bouwterrein. Volgens de indeling van het I.V.O.N. komt zij in meer dan honderdtwintig uurhokken voor, afgezien van de vindplaatsen waarvoor de hokindeling niet aangegeven kan worden; het opgeven van vindplaatsen blijft hier achterwege.

f. *brachyglossum* v. Soest: *ligulae breves, calathium paulo radians.*

Wassenaar, bij Maaldrift 1945 v. S. (h); voorts Waalsdorp, Loosduinen en Bilthoven, alle v. S. (h).

f. *involutum* v. Soest: *ligulae marginales involutae extus stria rubroviolacea notatae.*

Meijendel 1943 v. S. (h); voorts Waalsdorp en Raamweg bij den Haag, beide v. S. (h).

3. **Taraxacum simile** Raunkiaer 1906, Dansk Eksk. Fl. 2e ed.; Dt. 1921, Act. Fl. Sue. 1, c. icon. (pl. X).

Deze soort is onder de *Dissimilia* gekenmerkt door de volgende eigenschappen: pollen ontbreekt, de stempels zijn vrij donker (vuil-)geel; de buitenste omwindselbladen zijn afstaand, aan de top teruggekromd, breedgerand; de bladen zijn smal, smal driehoekig teruggericht-gelobd, de zijlobben zijn spits, de eindlob is verlengd pijlvormig. Bij het typische materiaal zijn de binnenste omwindselbladen zwak, maar duidelijk geknobbeld; bij het Nederlandse materiaal ontbreken de knobbels vrijwel.

Areaal: Z. Zweden, Denemarken, zeekust van Duitsland (Warnemünde), Nederland, Frankrijk.

Nederland: de Bilt, in de tuin van het Kon. Ned. Meteorologisch Instituut *B.* (h *v. S.*).

Drie andere soorten der *Dissimilia* zijn nog in Nederland gevonden; deze zijn niet beschreven en het is voorbarig dit reeds hier te doen.

Een ervan moet in bladvorm gelijken op *T. tanyolobum* Dt., Ber. Schweiz. Bot. Ges. 42 (1933), maar de hoofdjes zijn bij deze laatste soort groter, de buitenste lintbloemen meer roodpurper gestreept aan de buitenzijde, de bladstelen violetter. Daar ik nog geen inzage heb kunnen krijgen van het type-materiaal, resp. over geen afbeelding beschik, kan ik de samenhang dezer beide soorten onvoldoende nagaan; zij is op enige plaatsen bij Nijmegen aangetroffen door *Th. R.* (h. *K. & R.*).

Een tweede nieuwe soort, bij Arnhem (Onderlangs) gevonden, is onvolledig verzameld; zij is verwant met *T. dissimile* Dt.; in h. *v. S.* ligt zij onder de naam *T. rhenanum* m.

Een derde soort is enerzijds verwant met *T. pseudo-lacistophyllum* v. S. (*T. affine* Hagl. non Jordan), Bull. Rijkspl. t. Brussel 26 (1956), Ber. Schweiz. Bot. Ges. 60 (1950), anderzijds met *T. falcatum* Brenner, Med. Soc. Fau. Fl. Fenn. 34 (1921). Van de eerste verschilt zij door de bladvorm: de bladlobben zijn niet smal en niet zo langtoppig en rechtuitstaand, als bij *T. lacistophyllum.* Van de tweede verschilt zij door donkere stempels, smallere buitenste omwindselbladen, lange vruchtconus en het bezit van pollen; de plant is grover van bouw, maar de bladvorm doet er wel aan denken. Saarsoo, die duplicata zag, is zeker dat het geen *T. falcatum* is. Deze nieuwe soort is bij Venlo (Jammerdaalse heide) gevonden, *B.*, *Gr.* & *v. S.* (h.).

Het is zeer gewenst in Rijn- en Maas-gebied naar meer materiaal van deze soorten te zoeken.

SUBSECTIO FULVA CHRISTIANSEN (pro sect.).

4. **Taraxacum fulviforme** Dt. 1922, Rep. Bot. Soc. & Exch. Cl. Brit. Isles 6.— *T. dissimile* v. S., NKA l.c., non Dt.

Icones: v. S., NKA l.c. fig. 2 (s.n. *T. dissimili*); v. S., Bull. Rijkspl. t. Brussel 26 (1956) fig. 66.

In Nederland is deze soort voldoende van andere soorten te onderscheiden door de voor de *Fulva* kenmerkende vruchtkleur en door felpurperkleurige bladstelen, terwijl ook de hoofdnerf der bladen onderaan aldus is gekleurd; pollen is aanwezig, de stijlen en stempels zijn vrij donker; de buitenste omwindselbladen zijn aanliggend, de eindlob der bladen is vaak lang.

Areaal: algemeen in Z. Engeland, kuststreek van Nederland en België; ook in Z. Frankrijk.

Nederland (kaart Ib): in de zeeduinen op zonnige of lichtbeschaduwde plaatsen; Duindistrict tot in het Waddendistrict noordwaarts tot Texel, dat de noordgrens van het areaal vormt.

Texel, Westerduinen *Meeuse* (h L); aldaar en omgeving van de Koog *Hagl.* & *v. S.* (h); Beverwijk, Castricum en Wijk a. Z., alle *v. S.* (h); Noordwijk en Katwijk *de J.* (h) & *v. S.* (h); omgeving van Wassenaar en den Haag, vgl. NKA l.c., enz.; Kijkduin *v. S.* (h); Hoek van Holland *v. S.* (h); Wijde slik aan de Brielse Maas *Bakker* (h. IJsselm.); de Beer *De Langhe* (h); Rockanje *Sipkes* & *v. S.* (h); idem *Hagl.* & *v. S.* (h); Oostkapelle en Oranjezon *Lako* (h. L).

5. **Taraxacum fulvum** Raunkiaer 1906, Dansk Eksk. Fl. ed. 2.
Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 23, pl. IV.
Exsiccata: Dahlstedt II.9; IV. 6; IV. 51 (s.n. *T. brachycrani*); VI. 16, 17 (s. n. *T. brachycrani*); Lindberg 1415 (s. n. *T. brachycrani*), 1417, 1418.

De soort mist pollen en heeft vuilgele stempels, terracottakleurige vruchten; de buitenste omwindselbladen zijn ei-lancetvormig, witgerand en afstaand, min of meer geknobbeld; de bladen zijn driehoekig gelobd, vrij variabel van vorm, bleek tot zwak rood gesteeld. In de karakteristieke vorm, waarin deze soort in N. Europa optreedt, is zij in W. Europa nauwelijks gevonden; mogelijk schuilen onder het aldaar verzamelde materiaal enkele soorten, die nog nieuw te beschrijven zijn. Het materiaal van de Nederlandse en Vlaamse kust is vrij homogeen, de bladlobben zijn smaller, soms veel smaller dan normaal; het materiaal van Limburg heeft eveneens smalle bladlobben en heeft gele stempels.

Areaal: geheel N. Europa; Nederland, België, Frankrijk,Engeland.

Nederland: Katwijk-Noordwijk *de J.* (h); duin bij Watertoren den Haag *Boerboom* (h); Rockanje *Hagl.* & *v. S.* (h); Mellischet (L) *Gr.* & *v. S.* (h).

SUBSECTIO ERYTHROSPERMA DT. (pro sect.) EM. CHRISTIANSEN.

6. **Taraxacum agaurum** v. S. 1956, Act. Bot. Neerl. 5 — *T. laetum* v. S., NKA l.c., non Dt. — *T. soesteanum* Hagl. nom. nud.
Icones: v. S., NKA l.c. fig. 4 (s.n. *T. laeti*).

Door heldergele stempels, donkergele bloemen, groene bladsteel en aanliggende, sterkgehoornde buitenste omwindselbladen is deze soort van alle andere Nederlandse *Erythrosperma* te onderscheiden; de in NKA genoemde *T. laetum* komt in Nederland niet voor.

Areaal: Nederland, alleen in het Duindistrict tussen Loosduinen en Noordwijk (kaart Ic).

Op de in Act. Bot. Neerl. l.c. vermelde vindplaatsen is als aanvulling te geven: Katwijk *de J.* (h). De f. *tubulosa* v. S. is nog gevonden: Harstenhoek bij Scheveningen *Boerboom* (h.)

7. **Taraxacum brachyglossum** Dt. 1911, Ark. f. Bot. 10. — *T. erythrospermum* ssp. *brachyglossum* Dt. 1905.
Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 24, pl. VI.
Exsiccatum: Dahlstedt II. 1.

T. brachyglossum (fig. 1) heeft opvallend kleine vruchten minder dan 3 mm lang, met een kort-cylindrische conus; de buitenste lintbloemen zijn vrijwel altijd abnormaal ontwikkeld: kort en/of aan de top overlangs ingerold. De buitenste omwindselbladen zijn nauwelijks gerand, duidelijk purper aangelopen. Het blad is driehoekig gelobd, weinig getand, de eindlob is veelal min of meer pijlvormig en duidelijk spits.

De soort is reeds genoemd in NKA l.c. met de vermelding dat het materiaal van de vier opgegeven vindplaatsen uit de Wassenaarse duinen nogal variabel was, zodat mogelijkerwijs een nieuw te beschrijven soort hierop betrekking zou kunnen hebben. Inderdaad is dit juist gebleken: *T. silesiacum*, een jaar tevoren echter reeds gepubliceerd.

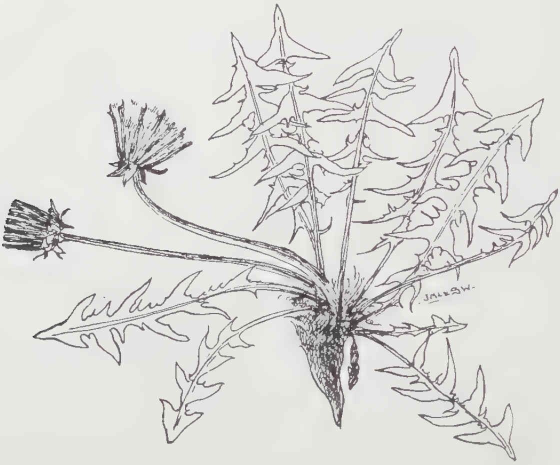


Fig. 1. *T. brachyglossum;* Soerel. $^1/_2$ ×

T. silesiacum heeft grotere vruchten met langere conus, goed ontwikkelde lintbloemen, iets meer gerande, meest bredere en minder gekleurde buitenste omwindselbladen. Bovendien mist zij pollen. Ten slotte is het blad van *T. silesiacum*, indien karakteristiek gevormd, opvallend door de zeer korte driehoekige eindlob met meest stompe top.

Areaal: Estland, Z. Zweden, Z. Noorwegen, Denemarken, N. Duitsland, België en misschien Zwitserland; aangevoerd in de Ver. St. v. Amerika.

Nederland:

Waddendistrict: Texel, Westerduinen *Hagl.* & *v. S.* (h).

Duindistrict: Beverwijk *v. S.* (h); Noordwijk-Katwijk *de J.* (h) & *v. S.* (h); Katwijk a. Z. *de J.* & *Th. R.* (h. *K.* & *R.*); idem *v. O.* (h); binnenduin bij Katwijk *de Wilde* (h); Kijfhoek-Bierlap *v. S.* (h); Meijendel *Boerboom* & *v. S.* (h), duin ten N. van den Haag *Boerboom* (h); Loosduinen-Monster, duinrand *v. S.* (h).

Binnenland: Ommen-Hardenberg, de Hongerige Wolf *K.* (h. *K.* & R.); Goor-Markeloo, legerplaats Oldebroek, 't Harde, Nunspeet-Soerel, alle *v. S.* (h); Soerel *Hagl.* & *v. S.* (h); Onderlangs, Arnhem *v. S.* (h); hoge rug langs de Maas bij Kessel *B.*, *Gr.* & *v. S.* (h).

8. **Taraxacum commixtum** Hagl. ex Hylander 1941, Fört. Skand. Växter. — *T. commutatum* Dt. 1921 nec Jordan 1852 (nec v. S. 1939).

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 11, pl. VII (s.n. T. *commutati*).

Evenals *T. agaurum* heeft deze soort (fig. 2) heldergele stempels; door rood gesteelde bladen wijkt zij b.v. van deze af. In habitus gelijkt zij meer op *T. lacistophyllum*, maar zij is in het algemeen forser en groothoofdiger; bij goed-ontwikkelde planten is de bladvorm zeer opvallend; de zijlobben zijn eerst versmald en dan naar de top toe verbreed. De omwindselbladen zijn meer aanliggend en breder gerand dan bij *T. lacistophyllum*. DAHLSTEDT beschreef de soort zonder pollen.

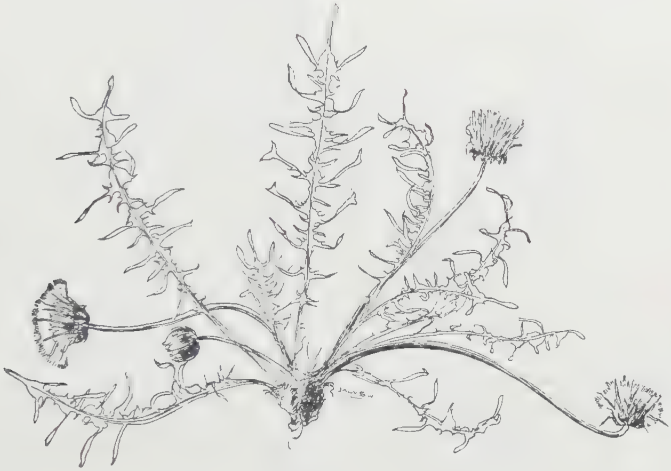


Fig. 2. *T. commixtum;* Egmond a. Z. 1/3 ×

Areaal: Z. Zweden, Denemarken en Bornholm, Nederland; eenmaal in Frankrijk.

Nederland: (kaart Id) in het Duindistrict tussen Egmond en Hoek van Holland, op lichtgrazige grond in de jonge duinen; éénmaal in het Waddendistrict gevonden.

Schiermonnikoog *Koolstra* & *v. d. Ploeg* (h); Egmond a. Z., Egmond-binnen en Castricum, alle *v. S.* (h); Amsterdamse Waterleidingduinen *Go.* & *v. S.* (h); algemeen tussen Noordwijk en Katwijk *de J.* (h), *v. O.* (h), *v. S.* (h); algemeen in de duinen van Wassenaar, Waalsdorp, Scheveningen en ten N. van den Haag *Boerboom* (h), *v. S.* (h), *de Wilde* (h); Westduinen ten Z. van den Haag en Hoek van Holland, beide *v. S.* (h).

9. **Taraxacum disseminatum** Hagl. 1947, Svensk Bot. T. 41, c. icon.

Deze voor Nederland nieuwe soort doet iets aan T. *scanicum* denken; opvallend zijn echter de brede, korte zijlobben der bladen met sterk convexe rug en met fijne lange tanden (fig. 3); de eindlob is vaak verlengd. Aan de bladrand en in de interlobia vindt men meest wat donkerpurperen kleuring. De buitenste omwindselbladen zijn duidelijk gerand en zeldzaam van zwakke hoorntjes voorzien; de stijlen en stempels zijn donker, in gedroogde toestand vrijwel zwart; de vruchten zijn (iets roodachtig-) bruin.

Areaal: Z. Zweden en Z. Noorwegen, oorspronkelijk waarschijnlijk met graszaad ingevoerd; Denemarken, Rügen, Nederland; Bohemen (exsicc. Baenitz!).

Nederland: enkel in het Duindistrict.

Wassenaar en Waalsdorp, beide *v. S.* (h); vermoedelijk met duinzand aangevoerd op een polderdijk op Rozenburg tegenover den Briel, *B.*, *Gr.* & *v. S.* (h).

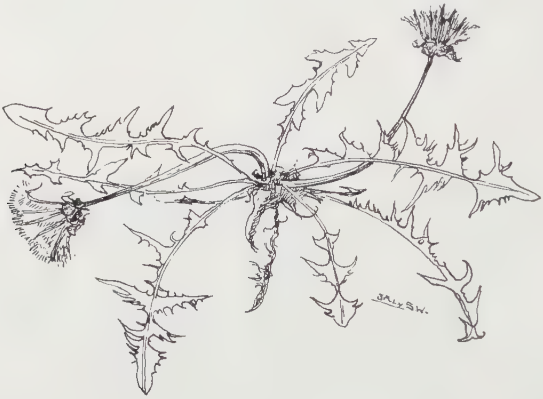


Fig. 3. *T. disseminatum;* Wassenaar. 1/2 ×

10. **Taraxacum dunense** v. S. 1956, Act. Bot. Neerl. 5. — *T. tenuibum* v. S., NKA l.c. non Dt.

Icones: v. S. ,NKA l.c. fig. 6 (s.n. T. tenuilobi); v. S., Bull. Rijkspl. t. Brussel 26 (1956) fig. 64.

De plant gelijkt in kenmerken, meer dan in algemene habitus, op *T. rubicundum.* De omwindselbladen zijn echter lancetvormig, aan de top teruggekromd; de hoofdjessteel is behaard; de bladvorm is afwijkend: de rechtuitstaande zijlobben zijn opvallend smal en in het midden het breedst; het donkerpurper van de bladsteel strekt zich ver tot in de hoofdnerf uit. In het algemeen is zij wat krachtiger van bouw dan *T. rubicundum,* al blijft het een zeer sierlijke plant.

Areaal: Vlaamse en Nederlandse zeeduinen in het Duindistrict (kaart IIIa). In Nederland is zij, als aanvulling op de gegevens in Act. Bot. Neerl. l.c., nog gevonden bij Castricum *v. S.* (h).

De in NKA l.c. vermelde *T. tenuilobum* Dt. komt in Nederland niet voor.

11. **Taraxacum lacistophyllum** Dt. 1911, Ark. f. Bot. 10.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 13, pl. VI; v. S., Bull. Rijkspl. t. Brussel 26 (1956) fig. 65.

Exsiccata: Dahlstedt II. 2; IV. 3,4; F. Schultz, Herb. norm. 45 bis (s.n. *T. off. var. arenarii*).

De soort is reeds vermeld in NKA l.c.; aan de aldaar gegeven beschrijving behoeft weinig te worden toegevoegd. In Nederland is verwarring mogelijk met *T. rubicundum,* vooral bij onvolgroeide exemplaren. *T. lacistophyllum* heeft onder het hoofdje behaarde i.p.v. kale stelen en zwakrode, althans niet diep-donkerpurperen bladstelen. In vruchttoestand zijn de soorten gemakkelijk kenbaar aan de vruchtkleur: helderbruinrood bij *T. lacistophyllum* en donkerroodbruin bij *T. rubi-*

cundum; zie verder onder *T. rubicundum*. Van *T. commixtum* verschilt *T. lacistophyllum* door vuilgele tot donkere stempels en door smallere, niet sterkgerande buitenste omwindselbladen.

Areaal: van Letland en gematigd N. W. Europa door W. Europa tot in N. Portugal en Z. Frankrijk; ook hier en daar in midden Europa.

Nederland (kaart II): uit NKA l.c. was de soort voor de omgeving van den Helder, Wieringen en uit het Duindistrict, vooral om Den Haag, aangegeven. Al zal de verspreidingskaart niet compleet zijn, ongetwijfeld mag gezegd worden dat *T. lacistophyllum* niet algemeen is, doch zich beperkt tot de zee- en rivierduinen, tot de zandige kusten van de voormalige Zuiderzee en hellingen van de zanddistricten langs de rivierdalen; ten slotte komt de soort aangevoerd voor met zand langs dijken e.d. Vrijwel alle op de kaart aangegeven vindplaatsen berusten op herbarium-materiaal, waarvan de opgave hier achterwege blijft.

12. **Taraxacum laetiforme** Dt. 1909, Bot. Not.

Iconus: Dt., Act. Fl. Sue. 1 (1921) pl X.

Deze voor Nederland nog niet vermelde soort (fig. 4) is gekenmerkt door bleke bladkleur en slechts zwakgekleurde bladsteel; de driehoekige bladlobben zijn vaak teruggericht; de buitenste omwindselbladen zijn smal en uitstaand; de bloemen zijn lichtgeel, voorzien van pollen, de stempels zijn vuilgeel. Het meeste gelijkt ze op *T. scanicum*, die echter een felrode bladsteel, donkergroene bladen, minder lichtgele bloemen en donkere stijlen heeft.

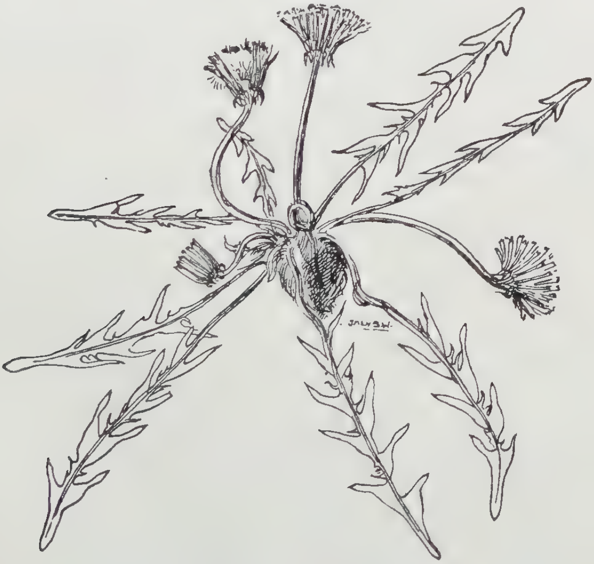


Fig. 4. *T. laetiforme;* Waalsdorp. 1/2 ×

Areaal: Z. Zweden, Denemarken en Bornholm, Nederland; onzeker voor Engeland.

Nederland (kaart IIIb): alleen in de zeeduinen.

Waddendistrict: Terschelling, op vele plaatsen in de duinen *W.* (h); Vlieland, Malgem *V. de Vries* (h W.); Texel, duinen bij de Koog en Westerduinen op verschillende plaatsen *Hagl.* & *v. S.* (h).

Duindistrict: Beverwijk, duin *v. S.* (h); Meijendel *de Wilde* (h); veelvuldig in de Wassenaarse, Waalsdorper en noordelijke Haagse duinen en Scheveningen, alle *v. S.* (h).

f. *citrina* v. Soest: *ligulae perpallide luteae, marginales extus stria purpurea notatae:* Waalsdorp 1954 *De Langhe* & *v. S.* (h).

13. **Taraxacum polyschistum** Dt. 1909, Bot. Not.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 14, pl. V; Hagl., Bot. Not., 1946 (f. *oelandicum* Hagl.).

Exsiccatum: Dahlstedt I. 8.

Deze soort heeft, evenals *T. lacistophyllum*, vrij lichtroodbruine vruchten, die echter tot onderaan ruw zijn; de buitenste omwindselbladen zijn eirond en breed-gerand; de hoofdjes zijn ook groter en donkerder geel dan bij de meeste andere *Erythrosperma*; de stijlen en stempels zijn donker van kleur; de bladlobben zijn driehoekig maar met verlengde top, vrij dicht opeengeplaatst.

Areaal: Gotland, Oeland; Nederland, België en midden Frankrijk, overal sporadisch.

Nederland: Duindal bij Den Haag, v. S. (h).

14. **Taraxacum proximum** Dt. 1911, Ark. f. Bot. 10. — *T. erythrospermum* ssp. *proximum* Dt. 1905.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 12, pl. I.

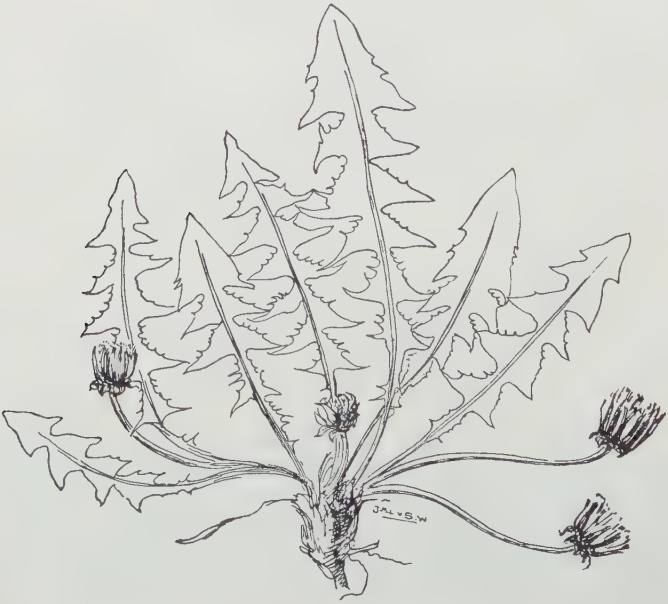


Fig. 5. *T. proximum;* Nieuwe Scheveningse Bosjes. 1/2 ×

Exsiccata: Dahlstedt I. 11; Lindberg 1424.

In habitus doet de soort (fig. 5) aan de *Vulgaria* denken, maar de gehele bouw is toch wel teerder, ofschoon b.v. *T. parvuliceps* Lb. (*Vulgaria*) evenzo teer is. In jonge toestand, als de zuiverbruine van een lange conus voorziene vruchten ontbreken, is zij moeilijk van de *Vulgaria* te scheiden; de buitenste omwindselbladen zijn ongerand, staan af met teruggebogen top; de voor de *Erythrosperma* zo kenmerkende hoorntjes of knobbels zijn maar spaarzaam ontwikkeld. *T. proximum* mist pollen, de stempels en het bovendeel van de stijlen zijn donker vuilgeel. De bladlobben zijn driehoekig, spits, met meer of minder recht afstaande onderkant.

Areaal: Finland en Baltische landen: midden en Z. Zweden, Denemarken, N. Duitsland (zeekust); Nederland en België.

Nederland: plaatselijk; evenals *T. scanicum* en *T. silesiacum* behoort zij meer tot de flora van het binnenland dan van het jonge duingebied in de kuststrook.

Duindistrict: bij den Haag in de door de plantsoendienst onderhouden bosgebieden: Bosjes van Zaanen en bosjes tussen Klein-Zwitserland en de Waalsdorper weg, beide *v. S.* (h); Nieuwe Scheveningse Bosjes *Hagl.* & *v. S.* (h).

Drents district: Urk *Bakker* (h. IJsselm.).

Gelders district: Waskolk bij Nunspeet *v. S.* (h).

Subcentreuroop district: Nijmegen, Sumatraplein en Bankastraat *Th. R.* (h. *K.* & *R.*); Wychen *J. J.* (h. NBV); Well *B.*, *Gr.* & *v. S.* (h); in h. *K.* & *R.* vermoedelijk van nog meer plaatsen uit de buurt van Nijmegen.

15. **Taraxacum rubicundum** Dt. 1911, Ark. f. Bot. 10. — *T. erythrospermum* ssp. *rubicundum* Dt. 1905.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 8, pl. I; v. S., NKA l.c. fig. 5.

Exsiccata: Dahlstedt I. 5; II. 1; Lindberg 1426.

In NKA l.c. is de soort voor Nederland aangegeven. De plant is fijn gebouwd, gekenmerkt door donkerrode bladstelen en kale hoofdjesstelen; het omwindsel heeft vrijwel aanliggende min of meer eivormige, duidelijk gerande buitenste blaadjes, die gehoornd zijn; de lichtgele bloemen bezitten in Nederland vrijwel steeds pollen, wat in Scandinavië minder het geval is.

Bij *T. lacistophyllum* is ingegaan op de verschillen met deze soort. Als kritisch moeten planten van *T. rubicundum* met behaarde hoofdjesstelen (f. *araneiferum* v. S.) en van *T. lacistophyllum* met kale hoofdjesstelen worden beschouwd; in zulke gevallen zal de vruchtvorm en de vruchtkleur beslissen.

De door Dahlstedt beschreven ssp. *monspeliense*, zie ook NKA l.c., schijnt niet meer als van belang te worden beschouwd.

Areaal: Finland en Åland; Z. Zweden, Denemarken, Duitsland tot in Oostenrijk; Nederland, België en Frankrijk, Engeland; aangevoerd in de Ver. St. v. Amerika.

Nederland: er zijn een aantal aanvullingen op de lijst in NKA l.c.

Waddendistrict: Texel, de Geul *Meeuse* (h. L); duin ten Z. van Huisduinen *v. S.* (h).

Duindistrict: Castricum, Egmond en Beverwijk, duinen, alle *v. S.* (h); Overveen *Buse* (h. L); Oosterveld *v. O.* (h); Noordwijk-Katwijk, duinen *de J.* (h) & *v. S.*

(h); Katwijk a. Z. *v. O.* (h); vele aanvullingen op de reeds gegeven vindplaatsen om Wassenaar, den Haag en Loosduinen (div. h); Hoek van Holland *v. S.* (h), terwijl de vroegere opgave van daar fout bleek; met duinzand te Delft aangevoerd! *v. S.*

Maasgebied: wellicht een afwijkende vorm, zie ook NKA l.c.: Plasmolen, Middelaar, Oeffelt, Gassel-Vogelshoek, leemgroeve Venlo, verzameld door verschillende combinaties van verzamelaars: *J. J.*, *K.*, *B. R.*, *Th. R.* (h. *K.* & *R.*, h. NBV).

16. **Taraxacum scanicum** Dt. 1911, Ark. f. Bot. 10.

Icones: Dt., Act. Fl. Sue. 1 (1921) fig. 16, pl. VIII.

Exsiccata: Dahlstedt III. 4; IV. 5 (s.n. *T. tenuilobi*).

Deze soort (fig. 6) bezit pollen en heeft vuilgele, vrij donkere stempels; de buitenste omwindselbladen zijn smal, vrij duidelijk gerand, vaak roodachtig en teruggebogen aan de top; de bladen zijn meest donkergroen en hebben rode stelen; de bladlobben zijn smal driehoekig, spits, meest sterk getand, de verlengde eindlob is vaak gespleten of sterk getand en met een tongvormig tamelijk stomp einde; de vruchten zijn donker-roodbruin. Van *T. laetiforme*, die er in habitus op gelijkt, verschilt zij door donkerder bladkleur, dieprode bladstelen, donkerder stempels; enkel bij zwak ontwikkelde planten is verwarring mogelijk; de vruchtkleur van *T. laetiforme* is lichter roodbruin. Voor verschil met *T. disseminatum*, zie aldaar.

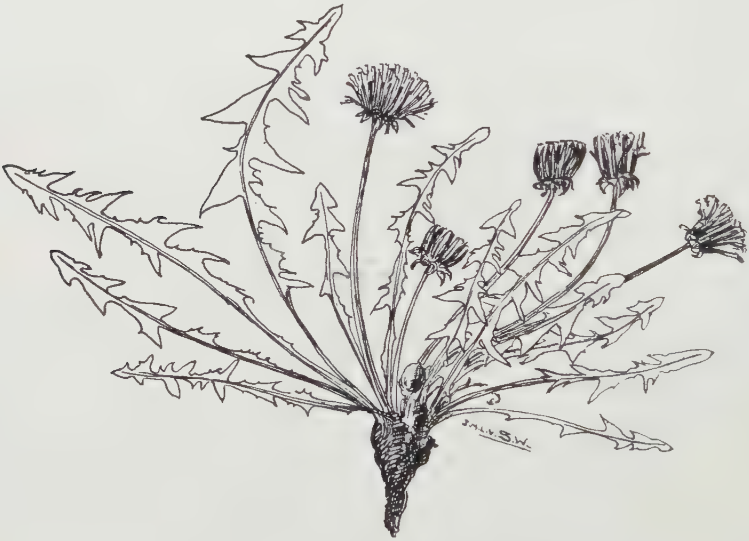


Fig. 6. *T. scanicum;* Meijendel. ½ ×

Areaal: Finland en Baltische landen, Z. Zweden, Denemarken en Bornholm, door Duitsland tot in Zwitserland; Nederland, België, Frankrijk, Engeland, Italië (kaart IV*b*); aangevoerd in Alaska en de Ver. St. v. Amerika.

Nederland: aansluitend aan het areaal, is *T. scanicum* nog niet in het

Noorden van het land gevonden; zij groeit op zandgrond, meer in het binnenland dan langs de kust in jonge duinen.

Drents district: Staart van Urk en de Voorst in de Noordoostpolder *Bakker* (h. IJsselm.).

Gelders district: Soerel bij Nunspeet en Zeist, beide *v. S.* (h).

Subcentreuroop district: Goor-Markeloo *v. S.* (h); in en nabij Nijmegen *K.*, *B. R.*, *Th. R.* (h); Jammerdaalse heide bij Venlo *B.*, *Gr.* & *v. S.* (h).

Kempisch district: Eindhoven *v. S.* (h); stuifzand ten O. van Wanssum *B.*, *Gr.* & *v. S.* (h).

Fluviatiel district: Maasrand ten N. van Kessel *B.*, *Gr.* & *v. S.* (h); duin bij Woensdrecht *Bakker* (h IJsselm.).

Duindistrict: Katwijk *de J.* & *v. S.* (h); op verschillende plaatsen in de binnenduinen van Wassenaar, den Haag en Loosduinen en in de jonge duinen van Meijendel en Waalsdorp, alle *v. S.* (h); Hoek van Holland, duin en zandgronden langs de Nieuwe Waterweg tot in de Nieuwlandpolder op verschillende plaatsen, *v. S.* (h); Bosduin en duinrand bij Rockanje *Sipkes* & *v. S.* (h); Groene strand *Hagl.* & *v. S.* (h); Wijde Slik aan de Brielse Maas *Bakker* (h. IJsselm.).

17. **Taraxacum silesiacum** Dt. ex Hagl. 1938, Bot. Not.
Exsiccatum: Callier 847 (s.n. *T. erythrospermi*).

Deze soort (fig. 7) doet aan *T. brachyglossum* denken, vgl. aldaar. Pollen ontbreekt; stijlen en stempels zijn vrij donker gekleurd. Opvallend zijn de bladen, wier eindlob breed deltavormig is met een basis die meest groter is dan de hoogte. De omwindselbladen zijn duidelijk gerand, dit in tegenstelling met *T. proximum*, die er in zwakke vormen op kan gelijken, doch zuiverbruine vruchten heeft; die van *T. silesiacum* hebben steeds een rode tint.

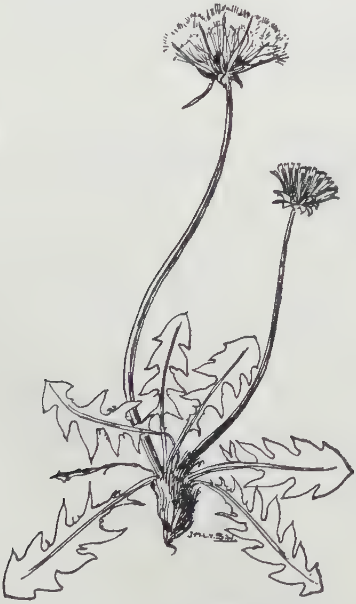


Fig. 7. *T. silesiacum;* Scheveningse Bosjes. $^1/_2$ ×

Areaal: Z. Zweden, Denemarken; midden Europa tot in Transsilvanië; Nederland, België en Frankrijk.

Nederland (kaart IIIc): evenals *T. scanicum* meer in het binnenland dan in de jonge zeeduinen, alwaar zij aangevoerd lijkt te zijn met grint langs paden, e.d.

Drents district: Texel, de Berg, plistocene grond *Hagl.* & *v. S.* (h); Zeegse stuifduinen *B.* & *v. S.* (h).

Gelders district: Legerplaats Oldebroek *Hagl.* & *v. S.* (h); op de Bergen bij Wessinge! *v. S.*; Doornspijk, op enige plaatsen om Nunspeet en bij de IJsselmeerkust bij Nunspeet en Hoophuizen, Nunspeet-Vierhouten, alle *v. S.* (h); kust bij Nunspeet *Bakker* (h. IJsselm.); Terlet *J. J.* & *Th. R.* (h. NBV, h. *K.* & *R.*, h. *v. S.*).

Subcentreuroop district: Nijmegen, op een paar plaatsen in de stad, bij Groesbeek, alle *Th. R.* (h. *K.* & *R.*); Broekhuizervorst, Looijerheide, Jammerdaalse heide bij Venlo, alle *B.*, *Gr.* & *v. S.* (h).

Fluviatiel district: Wijhe, oude rivierdijk *v. S.* (h); Epse, rivierduin *Gr.* & *v. S.* (h); Oeffeltse broek *J. J.* (h) & *Th. R.* (h. *K.* & *R.*).

Waddendistrict: Callantsoog-Huisduinen *B.* & *v. S.* (h).

Duindistrict: Aerdenhout, Oranjekom *Go.* (h) & *v. S.*; Valkenburg bij Katwijk *de J.* (h); Meijendel *Hagl.* & *v. S.* (h); id. *Vervoort* & *de Bruyn* (h. *de Wilde*), in grint bij de boerderij aldaar *Boerboom* & *v. S.* (h); Meijendel-Wassenaarse slag, in grint *Boerboom* & *v. S.* (h); Meijendel-Kievit langs de weg *v. S.* (h); oud barakkenkamp Waalsdorp, Scheveningse Bosjes, Pompstationsweg den Haag, Kijkduin, Hoek van Holland, Rockanje, alle *v. S.* (h).

18. **Taraxacum taeniatum** Hagl. ex Holmgren 1942, Blekinges Flora. — *T. commutatum* v. S., NKA l.c. nec Jord. nec Dt.

De soort (fig. 8) valt op door het ontbreken van stuifmeel en door

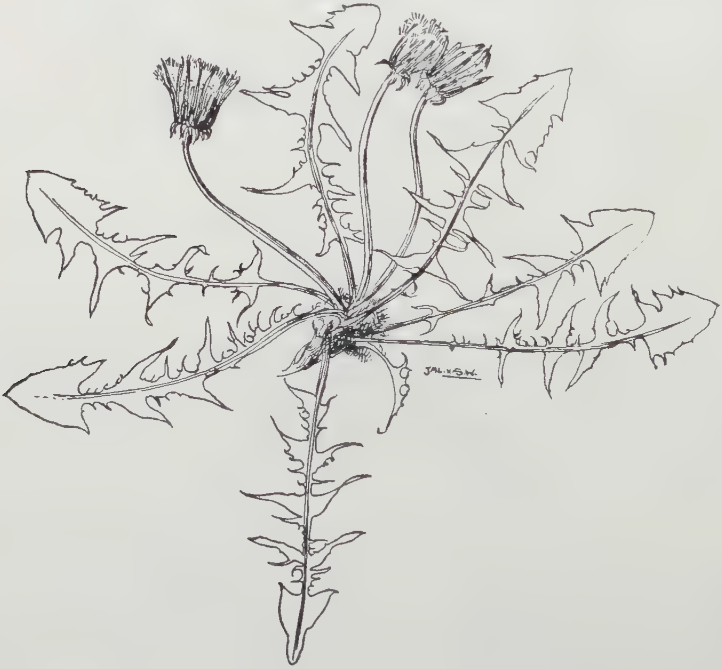


Fig. 8. *T. taeniatum;* Duindal, den Haag. ¹/₂ ×

geelgroene stijlen en stempels; de bloemen vallen na de bloei snel af; regelmatig bloeit deze soort ook in de herfst. De bladsteel is sterk purpergekleurd, de driehoekige bladlobben zijn grof en fijner getand, de buitenste omwindselbladen zijn bijna ingerold-teruggekromd, lichtpurper gekleurd; de hoofdjessteel is onder het hoofdje opvallend spinwebachtig behaard, maar ook lagerop vaak behaard. De vruchten zijn donkerroodbruin, vaak met maar weinig overmaat aan rood.

Areaal: Finland, Zweden, Noorwegen, Denemarken, kust van Nederland en België.

Nederland: (kaart IIId) in de jonge zeeduinen, zuidwaarts tot Voorne.

Ameland, Nes *v. d. Ploeg* (h); Texel, bij de Koog en in de Westerduinen *Hagl.* & *v. S.* (h); Huisduinen, Falga en tot Callantsoog *v. S.* (h); Wijk a. Z. en Castricum, beide *v. S.* (h); Amsterdamse waterleidingduinen, vgl. NKA l.c.; duin ten N. van Katwijk *de J.* & *v. S.* (h); veel in de Wassenaarse en Haagse duinen, vgl. NKA l.c., enz.; Hoek van Holland en Rockanje, beide *v. S.* (h); Groene strand aldaar *Hagl.* & *v. S.*!

Slechts driemaal zijn, enkel in de Waalsdorper duinen *v. S.* (h), planten van deze soort verzameld, die pollen bezaten.

Omtrent enkele in Nederland gevonden *Erythrosperma*-soorten bestaat voor mij nog onzekerheid.

Een ervan gelijkt in bladvorm op *T. proximum*, maar heeft pollen, lichtere stempels, bredere en breder gerande buitenste omwindselbladen; de vruchten (onrijp) zijn bruin: Nieuwenhoorn (Voorne) *B.*, *Gr.* & *v. S.* (h).

Een tweede doet aan *T. commixtum*, resp aan T. *brachyglossum* denken, het vrij talrijke materiaal uit de Wassenaarse duinen (h. *v. S.* en h. *Boerboom*) schijnt tot een nieuwe soort te behoren: stempels geel, pollen 0.

Een derde en vierde (?) soort komen overeen met soorten, als *T. glaucinum* Dt. en *T. glauciniforme* Dt.; de talrijke bladslippen zijn zeer smal en lang; de buitenste omwindselbladen breedgerand: veel bij Ierseke; Waalsdorp en Scheveningen *v. S.* (h).

Tabel der Nederlandse Obliqua en Erythrosperma

Taraxaca met een vrucht met lange cylindrische "conus", vaak roodachtig; omwindselbladen alle of ten dele met hoorntjes of, soms zwakke, knobbels.

1. Vrucht strokleurig tot lichtbruin 2
   Vrucht geelachtig rose, terracotta-kleurig, bruinrood tot donkerbruin 4
2. Blad bleekgroen, lobben kort; lintbloemen ingerold, door helrode aanloop oranje-achtig van kleur (*Obliqua*) . . . . 1. T. obliquum
   Blad gras- tot grijs-groen, lobben verlengd; lintbloemen vlak, lichtgeel (*Dissimilia*) 3

3. Bladlobben driehoekig, gekroesd, daardoor het blad niet vlak; omwindselbladen met hoorntjes, de buitenste vrijwel aanliggend . . . . 2. T. tortilobum

Blad vlak; omwindselbladen vrijwel zonder knobbels (stijl geel, buitenste omwindselbladen breed-gerand) . . 3. T. simile

4. Vrucht geelachtig rose tot terracotta-kleurig "fulvum" (*Fulva*) 5

Vrucht diep oranjebruin, bruinrood of donkerbruin (*Erythrosperma* s. str.) 6

5. Bladsteel felrood, buitenste omwindselbladen aanliggend . . . . 4. T. fulviforme

Bladsteel bleekrose of bruinachtig, buitenste omwindselbladen afstaand . . . . 5. T. fulvum

6. Stempels heldergeel 7

Stempels groengeel, vuilgeel tot zwartachtig 8

7. Bladsteel gevleugeld, groen (bladnerf zelden iets rood); buitenste omwindselbladen aangedrukt; bloemen donkergeel . . . . 6. T. agaurum

Bladsteel ongevleugeld, min of meer rood; buitenste omwindselbladen los aanliggend tot afstaand; bloemen lichtgeel . . . . 8. T. commixtum

8. Pollen ontbreekt 9

Pollen aanwezig 11

Opm. T. taeniatum is hoogstzelden met pollen, T. rubicundum zonder pollen in Nederland aangetroffen.

9. Buitenste omwindselbladen vrijwel ongerand; vrucht in rijpe toestand zuiver donkerbruin . . . . . 14. T. proximum

Buitenste omwindselbladen duidelijk gerand; vrucht oranje- tot roodbruin 10

10. Stempels groenig; buitenste omwindselbladen lichtpurper, teruggekromd . . . . 18. T. taeniatum

Stempels zwartachtig; buitenste omwindselbladen groen, aanliggend tot afstaand . . . . 17. T. silesiacum

11. Hoofdjesstelen kaal; buitenste omwindselbladen aanliggend . . . . 15. T. rubicundum

Hoofdjesstelen onder het hoofdje behaard; buitenste omwindselbladen aanliggend tot afstaand 12

12. Bladsteel en onderste deel van de hoofdnerf intensief donkerpurper . . . . 10. T. dunense

Bladsteel bleek, lichtpurper of rose 13

13. Lintbloemen kort en bovenaan meest ingerold; hoofdje nietstralend . . . . 7. T. brachyglossum

Lintbloemen vlak; hoofdje stralend 14

14. Eindlob driehoekig tot iets pijlvormig, weinig getand 15

Eindlob niet driehoekig, maar verlengd en vaak sterk ingesneden en getand 16

15. Buitenste omwindselbladen lancetvormig, smalgerand . . . . 11. T. lacistophyllum

Buitenste omwindselbladen breed, eivormig, breedgerand . . . . 13. T. polyschistum

16. Stempels vuilgeel, bladsteel bleek tot rose . 12. T. laetiforme
    Stempels donker; bladsteel purper. 17
17. Blad meest donkergroen, lobben kort en grofgetand, zonder opvallend convexe rug; vruchten rood- tot oranje-bruin. . . . . 16. T. scanicum
    Blad lichtgroen, lobben fijngetand en t.d. met sterk convexe rug; vruchten bijna zuiver bruin . . 9. T. disseminatum

SUMMARY

A revision of Taraxacum sect. Obliqua Dt. and sect. Erythrosperma Dt. em. Lb. for the Netherlands is given, regarding an old one by the author in Nederlandsch Kruidkundig Archief 49 (1939). Eighteen species are considered, pictures and maps are given.

OBLIQUA

1. T. obliquum (Fr.) Dt.+: sea dunes southward to the isle of Voorne; T. platyglossum Raunk., mentioned earlier, has not been found in the country.

ERYTHROSPERMA

Dissimilia

2. T. tortilobum Florstr.: common; f. brachyglossum m. and f. involutum m. are described.
3. T. simile Raunk.++: one locality in the central part of the country (new). Three other species, probably new and still to be described, appear in the eastern part of the country.

Fulva

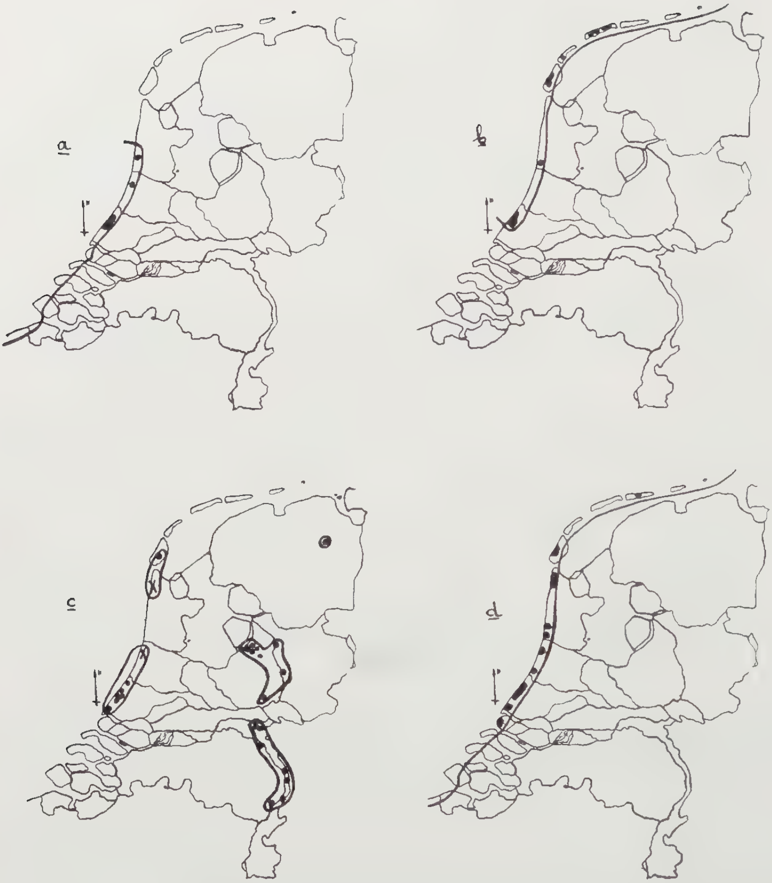
4. T. fulviforme Dt.+ (T. dissimile in NKA l.c.): sea dunes northward to the isle of Texel; T. dissimile Dt. is probably not indigeneous.
5. T. fulvum Raunk.: few localities, a form slightly different from the typical one.

Erythrosperma s. str.

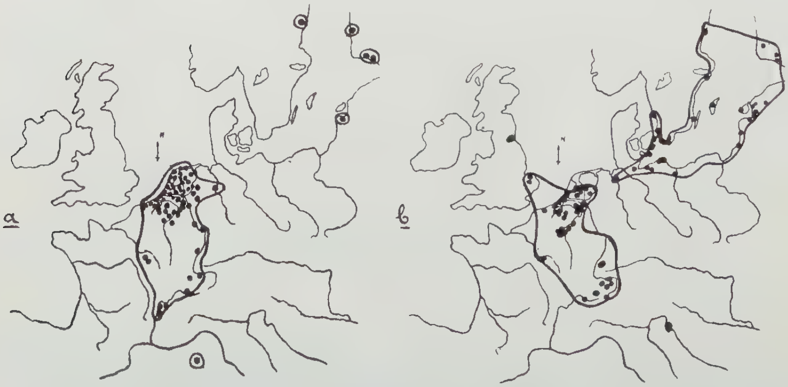
6. T. agaurum v. S.+ (T. laetum in NKA l.c.); sea dunes only between Loosduinen and Noordwijk; T. laetum is not indigeneous.
7. T. brachyglossum Dt.: few localities dispersed through the country.
8. T. commixtum Hagl. ex Hyl.+: sea dunes southward to Hook of Holland (new).
9. T. disseminatum Hagl.+: three localities nearby the sea coast (new).
10. T. dunense v. S.+ (T. tenuilobum in NKA l.c.): sea dunes northward to Castricum; T. tenuilobum is not indigeneous.
11. T. lacistophyllum Dt.: rather common.
12. T. laetiforme Dt.+: sea dunes southward to the Hague (new); f. citrinum m. is described.
13. T. polyschistum Dt.+: one locality (new).
14. T. proximum Dt.++: few localities dispersed through the country (new).
15. T. rubicundum Dt.: mainly in the sea dunes.
16. T. scanicum Dt.++: rather common (new).
17. T. silesiacum Dt. ex Hagl.++: rather common (new).
18. T. taeniatum Hagl. ex Holmgr.+ (T. commutatum in NKA l.c.): sea dunes southward to the isle of Voorne.

It thus appears that 9 species + are restricted to the sea coast, representing a group of more or less atlantic character; one of them is endemic (T. agaurum); two of them reach a northern, five a southern limit in the Netherlands.

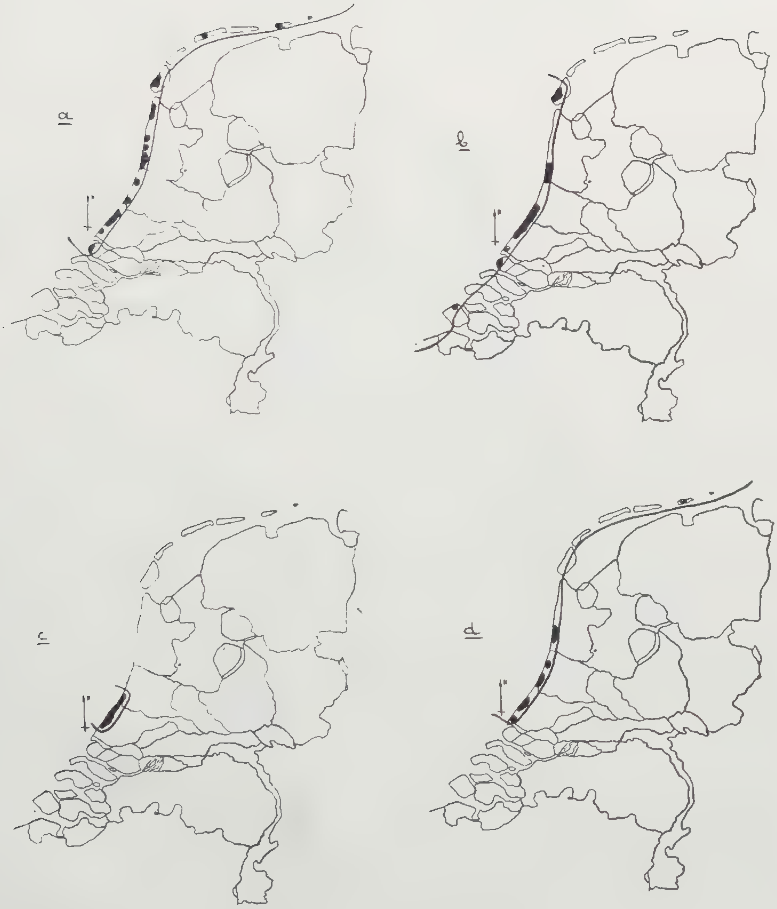
Of the others, four ++ belong essentially to the flora of the interior, representing a group of central and north european distribution.



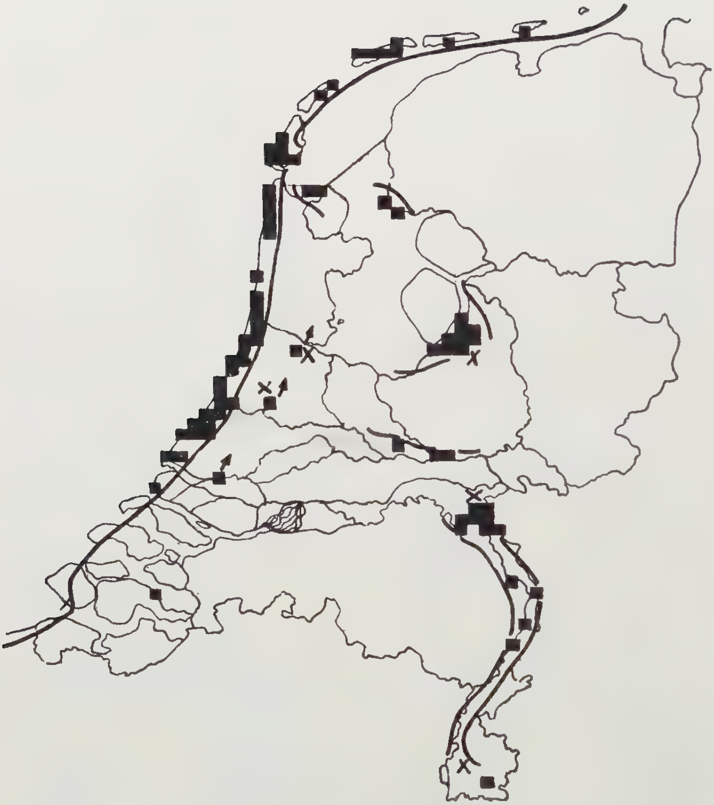
Kaart III. a: *T. dunense;* b: *T. laetiforme;* c: *T. silesiacum;* d: *T. taeniatum.*



Kaart IV. a: *T. tortilobum;* b: *T. scanicum*, voor het N.O. deel van het areaal zijn de gegevens overgenomen uit Haglund, Svensk Bot. T. 41 (1947) Abb. 3.



Kaart I. a: *T. obliquum;* b: *T. fulviforme;* c: *T. agaurum;* d: *T. commixtum.*



Kaart II. *T. lacistophyllum.*

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ON THE DISTRIBUTION OF CAREX AQUATILIS WAHLENB.

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(*received January 12th, 1957*)

The boreal *Carex aquatilis* was discovered nearly ten years ago in the Netherlands, in the provinces of Groningen and Drente (the northern part), in the north of this country. In the herbarium of the Royal Botanical Society of the Netherlands some older specimens from this area are preserved, erroneously identified by the collectors as *C. acuta* L. or *C. gracilis* Curt. (Kern and Reichgelt, 1947). The stations in the north of the Netherlands were the southernmost known.

Outside the Netherlands the area of its distribution in Europe comprises Ireland, West and North England, Scotland, Iceland, Norway (to the south as far as near Oslo), Sweden (to the south it becomes rarer), Finland, Esthonia (near Reval) and North Russia (as far as Leningrad). Between the stations in the above-mentioned countries and those in the Netherlands a disjunction occurs, for *C. aquatilis* is not recorded from N.W. Germany and Denmark (Andreas, 1951). Because of the disjunct area and the occurrence of fossil remains in layers, belonging to the glacial period Miss Dr. Ch. H. Andreas (1951, 1953) considers *C. aquatilis* in the Netherlands as a glacial relic.

In 1955 the present writer found *C. aquatilis* in the central part of the Netherlands near Wanneperveen (N.W. Overijssel) and Kolderveen (S.W. Drente). In this peaty area the species grows at the side of ditches, in marshy spots in pastures and in pools, more or less abundantly and mostly in the company of *Carex acuta* L., *C. nigra* (L.) Reichard and *C. rostrata* Stokes. In 1956 the species was discovered in and near "Lindevallei", between Peperga and Wolvega (province of Friesland), in hardly fordable marshland. *C. aquatilis* grows here in large numbers and in the company of *C. acuta* and *C. rostrata*. Moreover, I found the species this year to the east of Berkum near Zwolle (province of Overijssel), at the side of a ditch in peaty grassland. The last place is the southernmost station known at the moment (Fig. 1).[1]

During a visit to the Netherlands in the summer of 1955 *C. aquatilis*, which was unknown in Germany, was shown to the German botanist Alfred Neumann. On his journey back to Germany he succeeded in finding the species near Ruinerwold (province of Drente). Moreover he discovered the plant at several places in N.W. Germany (East Friesland, Oldenburg, to the east of Bremen). In the herbarium of Trentepohl he found erroneously identified specimens of *C. aquatilis* from Oldenburg, collected in 1793–'94. Neumann succeeded in finding the species again on the "classic station" of Trentepohl. In addition he learned from a study of herbarium material that *C. aquatilis* had been collected in the former East Prussia (in a letter of 6 April 1956). In 1956 the present writer collected the species near Südgeorgsfehn in East Friesland, Germany, at the side of a canal in a peat area.

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[1] After this article had gone to press Dr. S. J. van Ooststroom and Mr. Th. Reichgelt discovered in the "Rijksherbarium" at Leyden material of *C. aquatilis*, originally identified as *C. gracilis* and collected by Kloos along the Reest between Meppel and Yhorst in 1917.

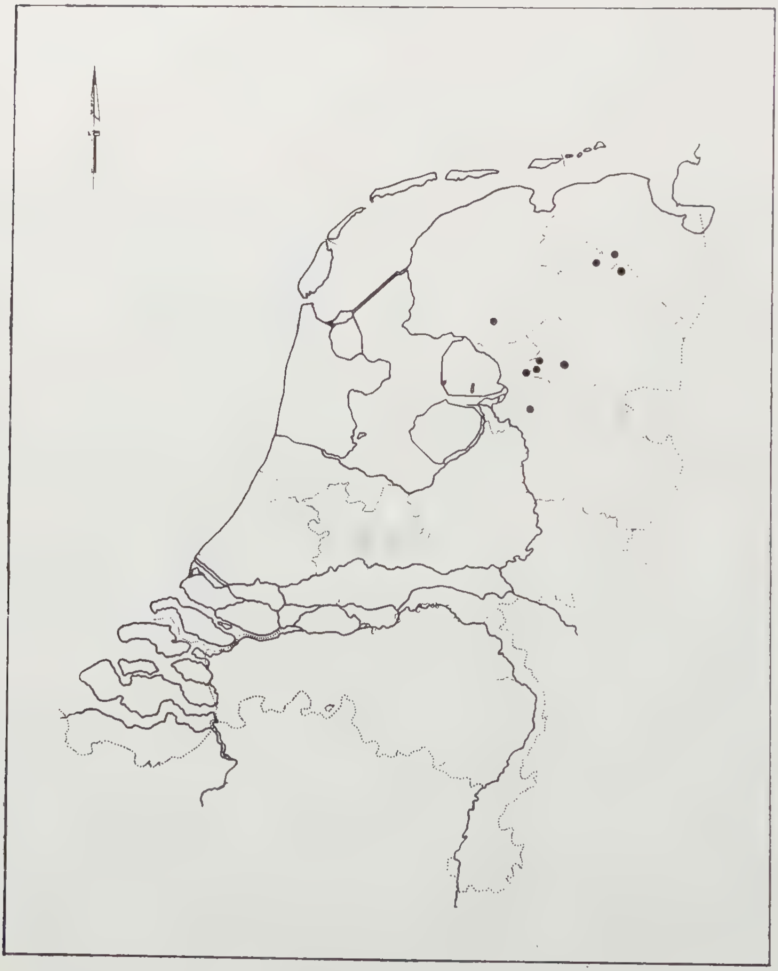

Fig. 1. Distribution of *Carex aquatilis* Wahlenb. in the Netherlands

Apparently *C. aquatilis* has been overlooked in Germany. In my opinion the species may also occur in Denmark. If this proves to be the case *C. aquatilis* in the Netherlands should not be considered as a glacial relic. Then the stations in this country would be the southern border of an unbroken area of distribution.

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A REVISION OF THE GENUS LINDSAEA IN THE NEW WORLD WITH NOTES ON ALLIED GENERA

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(*received March 21st, 1957*)

A. GENERAL PART

1. Introduction

The undertaking of the present study suggested itself to the author when, during the identification of ferns from Suriname with Posthumus' treatment (1928), it became evident that the species of the genus *Lindsaea* were particularly poorly understood. As it proved to be impossible to elucidate the status of the species from that region only, without a survey of those from adjacent regions, it was decided that a revision of all New World species was indicated. It was possible to restrict the study largely to the representatives in that part ot the world, as there is not a single species occurring in both hemispheres. This, of course, does not imply that the Old World species have been completely left out of account; as a matter of fact, reference is made to them repeatedly in the present paper, especially where generic limits are concerned; but it would be altogether too big a task to complete a revision of the whole genus. Probably close to 3/4 of all species are restricted to the Asiatic-Oceanic region.

No really complete revision of the genus has ever been given, apart from Hooker's treatment in the Species Filicum (Vol. I, 1844/46), and Hooker & Baker's Synopsis Filicum (1868, 1874). Diels (1902) gave only a superficial synopsis of the principal species. The situation is by no means better as far as the neotropical species only are concerned; the treatments are unsatisfactory, with ambiguous keys, as Baker's (1870, in Flora Brasiliensis), and, as stipulated above, in Posthumus' Ferns of Surinam, even, if only a small number of species are involved, e.g. in Maxon's Pteridophyta of Porto Rico (1926).

It is hoped that the present revision helps to clear up the taxonomy of this rather intricate genus. The author realizes that some problems still remain to be solved. To several of them cytotaxonomic studies would presumably contribute most valuable data. This applies particularly to *Lindsaea quadrangularis* and its relatives and to the diverse forms united under *L. stricta.*

Acknowledgements. The author wishes to express his deep gratitude to Dr. Rolla M. Tryon, Jr., and Dr. Alice F. Tryon, under whose guidance and with whose kind help this study was started, to Prof. Dr. J. Lanjouw, at whose institution and under whose supervision it was completed, and to Dr. Warren H. Wagner, Jr., for his constructive criticism of the general part.

2. HISTORY OF THE GENUS.

The genus *Lindsaea* was described in extenso by DRYANDER (1797), although it had been included a few years before in a paper by J. E. SMITH (1793) as "Lindsaea Dryandri (inedit.)" which constitutes valid publication. However, for none of the three species listed the combination under the new genus was actually made; this was left to Dryander's publication, which included a total of 10 species, 7 of which were published as new; the others were transferred to the new genus from *Adiantum*. The similarity in general aspect of many species of *Lindsaea* to species of *Adiantum* is indeed striking (for a more detailed account, see p. 132). Nevertheless, even apart from the fertile structures, there are quite a number of differences to be observed without the aid of a microscope, many of which were overlooked for a long time, so that FÉE still wrote (1865): "Ces fougères ont le port des Adiantum, dont elles ne diffèrent guère que par le mode de déhiscence des sporothèces . . .". It is even more surprising that careful authors like Swartz and Aublet were deceived by the similarity; the latter author, when publishing his "*Adiantum guianense*" (1775), which, as shown by his good plate, is beyond doubt a *Lindsaea*, was so convinced that he was dealing with an *Adiantum* that he described the sorus as "le bord supérieur de chaque portion est membraneux, réplié en dessous pour couvrir les fleurs qui y son placées", apparently without careful study of the actual condition.

Soon after the publication of Dryander's paper, the validity of the genus seems to have been generally accepted, and many authors working in the nineteenth century described new species, particularly Swartz, Desvaux, Klotzsch, G. Kunze, and Fée. However, many of these authors did not understand each other's, or even their own species, and already at that time, with still a comparatively small number of names to be kept in record, many misidentifications occurred. One of the few authors of that time who seems to have had a good understanding of at least the neotropical species was Klotzsch (chiefly in his publication of 1844); rather few of his species had to be cancelled later. Hooker's treatment in the Species Filicum did not do as much injustice to the naturalness of the genus as in many other cases, but his concept of species was also poor. The unsatisfactory condition in such treatments as BAKER's (1870) and POSTHUMUS' (1928) has already been commented on. This condition can be said to have prevailed practically up to present times. During the author's studies, large portions of the material sent to him on loan, sometimes close to 3/4, were incorrectly named, and at least part of the correct identifications were due to the fact that many authors dumped all material they could not readily match in *Lindsaea lancea* (or "*trapeziformis*"), which is, indeed, the commonest species. Furthermore, it seems that apart from usually very inadequate descriptions, the confusion of the species was enhanced by the existence of several suggestive names; thus all specimens with small rigid pinnules were called *L. stricta*, specimens with quadrangular stipe became *L. quadrangularis*, etc., regardless of other characters. Among modern authors who studied the genus, Hieronymus seems to have been one of the few who understood which characters were of importance for distinguishing the species and which were not, as can be seen in his annotations on the specimens in the Berlin herbarium; unfortunately he published very little on the genus (his most important paper was in 1920.) On the other hand, Rosenstock, who wrote on the genus several times, describing new forms and making new combinations (e.g. 1906), and who distributed large numbers of specimens in his fern exsiccatae from South Brazil and Costa Rica, rather helped to increase the confusion.

To convey an impression of the number of species known and recognized in the course of time, the following figures may be given. From Dryander's original publication which included 10 species, 6 of which were from the New World, the number increased to 20 neotropical ones in HOOKER's Species Filicum (1844/46). FÉE (1852) listed 25 species from the Western Hemisphere; BAKER (HOOKER & BAKER, 1874) recognized only 15. DIELS (1902) credited the genus with only 30 species, of which about 1/3 (!) was said to occur in America, although Jenman only three years before had listed 20 from the British West Indies and British Guiana alone. This progressive lumping was somewhat checked by CHRISTENSEN (1906), who recognized in his Index Filicum 27 neotropical species, which number was increased to 37 in the subsequent supplements (until 1934). Of these, 25 are maintained on the species-level in the present treatment; several others listed by him as synonyms are recognized as valid species.

Hitherto, 96 names have been published on the species-level. Of these, 33 are retained in this study, 6 are treated as taxa of lower rank, 36 as synonyms, 13 are excluded from the genus, and the application of 8 remains uncertain, or the species to which they apply are of doubtful validity. In addition, 11 are published as new, and one previously published in a lower rank is raised to species-rank, which brings the total number of species in the New World to 45.

The generic limits have fluctuated comparatively little. Of Dryander's 10 original species, all are still maintained in the genus, although some with different epithets. The highly dissected species which lack the dimidiate pattern of pinnules long considered as typical for the genus were at first put in *Davallia*, where they were retained by some authors until about 80 years ago (e.g. in the second edition of Hooker & Baker's Synopsis Filicum, 1874). Other authors included them in *Odontosoria* or *Sphenomeris* ("*Stenoloma*"), where several of them remained till present times (some of them were transferred to *Odontoloma* and *Schizoloma*, not recognized here). These genera were, however, often associated with *Lindsaea*, either as close relatives within the Davallioid ferns, or as a separate group; certain authors included even all of them in *Lindsaea* (CHRIST, 1897; PÉREZ ARBELÁEZ, 1928). Only few authors (e.g. FÉE, 1852) grouped the dimidiate and less dissected forms with more or less continuous sori together and placed the highly compound ones in a quite different group, not even close to the Lindsaeoids.

3. THE GROUP OF LINDSAEOID FERNS

Although the name "*Lindsaeaceae*" or "*Lindsaeeae*" appeared considerably earlier (probably for the first time used by PRESL, 1836), the group as such can be said to have been established in a truly natural circumscription by CHRISTENSEN (1938). It had been separated before from the Davallioids, with which *Lindsaea* was most often associated by earlier authors, but was then made to include only *Lindsaea* itself and a few very closely allied genera such as *Isoloma* and *Schizoloma* (e.g. FÉE, 1852), which were sometimes united with it. To Christensen goes the merit for recognizing the affinity of *Tapeinidium*, *Sphenomeris* and *Odontosoria* with *Lindsaea* only, not with *Davallia*, with which they had been placed on account of their short sori with more or less pouch-shaped indusia. Christensen did, however, still include a few genera in the group, although with misgivings, that are now considered members of other groups, namely, *Taenitis*, *Platytaenia* (united by Copeland with the former), *Diellia*, and *Dictyoxiphium*. Copeland retained *Taenitis* and the allied genus *Syngramma* in the Linsaeoid group of his *Pteridaceae*, mainly because of supposed relationship between *Taenitis and "Schizoloma" (Schizolepton)*, but HOLTTUM's arguments (1947, p. 156) for inclusion of the two genera in the Gymnogrammoid ferns seem to be much stronger. The Asplenioid affinity of *Diellia*, already suspected by Christensen and assumed by COPELAND (1941, p. 161; 1947, p. 168) was firmly established by WAGNER (1952b, 1953). *Dictyoxiphium*, for a long time included in the Lindsaeoid ferns as a very aberrant member with "venatio anaxeti", may be safely referred to the Tectarioid group (see COPELAND, 1941, p. 160; 1947, p. 135; and HOLTTUM, 1947, p. 153).

The genus *Ormoloma* was described by Maxon in 1933; he only pointed out the differences from *Saccoloma*, where the type-species had usually been placed before, without committing himself as to its place in the system. CHRISTENSEN (1938), CHING (1940) and HOLTTUM (1947) placed it near *Saccoloma*, but COPELAND (1947) correctly pointed out its close alliance to *Lindsaea*.

The following genera should be retained in the Linsaeoids: *Tapeinidium*, *Isoloma*, *) *Schizolepton* (see p. 11), *Odontosoria*, *Ormoloma*, *Sphenomeris*, and *Lindsaea* itself. The three first-named genera are confined to the Eastern Hemisphere, the fourth and fifth to the Western, and

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*) Dr. M. A. Donk in an unpublished m.s. which he very kindly made available to the writer pointed out that *Isoloma* J. Smith cannot be typified by the Lindsaeoid fern *I. divergens* (Roxb.) J. Sm., but rather by *Lindsaea lanuginosa* Wall., a species of *Nephrolepis*. The genus that comprises *I. divergens* should bear the name *Guerinia* J. Smith. As his discussion has not yet been published and as the name *Isoloma* is currently applied to the Lindsaeoid genus, it is here still used in that sense.

Lindsaea and *Sphenomeris* are represented in both. To these has probably to be added an undescribed monotypic genus based on *Schizoloma stortii* v.A.v.R. which will be discussed elsewhere, and perhaps also an additional genus to accomodate *Lindsaea walkerae* Hooker. Contrary to HOLTTUM's opinion (1947, 1954), and in accordance with CHRISTENSEN (1938) and COPELAND (1947), the genus *Schizoloma* Gaud. (based on *Lindsaea ensifolia* Sw.) is not recognized here, although it is maintained in a restricted sense as a subgenus, with some doubt as to its tenability.

The Lindsaeoid ferns may be characterized as follows: Small to medium-sized ferns, terrestrial, occasionally scandent or epiphytic. Rhizome creeping or climbing, solenostelic or with a special kind of protostele (*Lindsaea*-type), clothed with scales, usually mixed with reduced, ± hair-like, but always flattened scales, sometimes these reduced scales only present; the scales non-peltate, entire, with very few exceptions not clathrate. Petioles non-articulate, with one U- or V-shaped vascular strand (two reported in *Tapeinidium*), ± persistently scaly at the base only. Lamina very variable, simple to decompound, rarely dimorphous, anadromic, in mature condition seemingly glabrous but thinly clothed with microscopic, mostly two- or three- (rarely more) celled hairs (see p. 32). Petiole and rachises with very few exceptions sulcate on the adaxial side, the groove bordered by ridges which are continuous with those on the axes of higher order and with the thickened edge of the ultimate divisions at least on the basiscopic side. Pinnae and pinnules non-articulate (except in *Isoloma*), attached on the margin of the adaxial side of the rachis. Veins dichotomously branched, free, or less often anastomosing, without included veinlets; a midrib mostly absent. Sori indusiate, terminal on the veins (occasionally slightly decurrent along them), inframarginal, the part of the lamina projecting beyond them without veins ("upper indusium"), the receptacle formed by the broadened end of one vein or by a commissure uniting from two to all the veins of an ultimate segment (pinnule) or of half or the whole lamina. Indusium fixed by its base or its base and sides, opening towards the margin, al least the distal half of one layer of cells. Sporangia long-stalked, the stalk at least just below the head consisting of three rows of cells; paraphyses present in some (all?) species, ± similar to the hairs of the vegetative parts. Annulus continuous or mostly interrupted by the stalk, mostly slightly oblique, with 8–22 indurated cells; a stomium of 2–6 cells mostly differentiated; spores smooth or almost so, without a perispore, monolete or trilete.

Nothing seems to be known about the gametophyte (see STOKEY, 1951).

4. COMMENT ON THE GENERA

The monotypic genus *Schizolepton* (*Schizoloma* sensu COPELAND, 1947), *Ormoloma* with two species, and *Odontosoria* (in MAXON's restricted and certainly most natural circumscription, 1913) with ten, seem to be well-defined genera. The same is true for *Isoloma*, from which genus should be excluded *Lindsaea walkerae*, referred to it by Presl, on account of the non-articulate pinnae, and the species sometimes called *Isoloma* *lanuginosum*. This was for a long time included in *Isoloma*, and recently (1952) Tardieu-Blot argued that it should be kept there. It is, however, a *Nephrolepis*, and not at all closely allied to the Lindsaeoid ferns, as shown by the ciliate rhizome-scales, the scaly rachis, the distinctly hairy leaf-tissue, the different structure of the rachis, and the very conspicuous hydathodes often covered with small pellets. The only characters shared with *Isoloma* are the articulate pinnae (found throughout *Nephrolepis*), and the sorus; and the latter character alone is not sufficient to warrant inclusion in *Isoloma*, probably not even exclusion from *Nephrolepis*. Tardieu-Blot's first group of *Isoloma* consists of aberrant species of *Nephrolepis*, and her second group is true *Isoloma*. The differences between the two groups, stressed by herself (l.c., p. 331) in the writers' opinion show the unnaturalness of *Isoloma* as defined by her. Her opinion that "Le genre *Isoloma* est incontestablement un passage entre les *Lindsaea* et les *Nephrolepis*" is not shared by the writer; *Isoloma* and *Nephrolepis acutifolia* (*Isoloma lanuginosum*) in his opinion both constitute specialized, in certain ways analogous, offshoots of quite different groups of ferns.

The genus *Schizoloma* Gaudichaud has been defined in various ways. It is difficult to understand what Gaudichaud had in mind when he described it; his description (1824, p. 507) is: "sori lineares, continui, marginales; indusium duplex exterius dehiscens", and fits several different forms of Lindsaeoid affinity. Of Gaudichaud's three original species, two were subsequently removed to other genera, which justifies the selection of the third, *S. billardieri*, as type-species, rather than *S. cordatum*, maintained as such by Copeland (1947). Alston (1956, p. 23) published *Schizolegnia* as a new name for *Schizoloma* (as currently understood, based on *Lindsaea ensifolia*), arguing that *Schizoloma* in this sense did not contain any of Gaudichaud's original species; but this is not so, as *Schizoloma billardieri* Gaud. is a heterotypic synonym of *Lindsaea ensifolia* Sw. (*Schizoloma ensifolium* (Sw.) J. Sm., and Alston's name is superfluous.

Schizoloma has been made to include several species removed from *Lindsaea*, sometimes also from *Isoloma*, by later authors; it was defined in such a way as to accomodate all forms with equal-sided rather than cuneate (*Odontosoria*) or dimidiate (*Lindsaea*) blades or segments, e.g. by Diels (1902). In this circumscription it contained quite diverse and not at all closely related elements, a.o. the two well-known simple-leaved species of *Lindsaea*, *L. reniformis* and *L. sagittata*, which, as is shown in this revision, have their natural place among the neotropical Lindsaeas with a large terminal pinnule. Holttum (1954) defined *Schizoloma* as including all species having equal-sided, non-articulate pinnae, or being bipinnate with the primary pinnae gradually decreasing in size and complexity towards the top of the leaf. This, however, makes delimitation towards *Sphenomeris* very difficult, as Holttum himself observed (l.c., p. 341); moreover, there are closely related species (in the New World *L. pendula* and *L. meifolia*) which, by this definition, would go in different genera.

In the present author's opinion, *Schizoloma* can be maintained on the basis of the combination of anastomosing veins with equal-sided pinnae (*L. ensifolia*, *L. vieillardii*, *L. macrophylla*) or with long undivided pinna-apices (*L. heterophylla*); but it is possible that future work on the species from the Indo-Malayan region and New Caledonia, where most representatives of this type are found, will show that even in this reduced sense the group is untenable. Most species referred to *Schizoloma* should be put or put back in *Lindsaea*, except *S. cordatum*, the only species of the monotypic genus *Schizolepton* Fée, all species with articulate pinnae which constitute *Isoloma*, and *S. stortii* (perhaps also *S. walkerae*) as discussed above.

A more intricate problem is the separation of *Lindsaea* and *Sphenomeris*.*) Usually, in floras and handbooks (e.g. DIELS, 1902, BACKER & POSTHUMUS, 1939, TARDIEU-BLOT & CHRISTENSEN, 1939, COPELAND, 1947, etc.) the following kind of key is found;

a. Segments dimidiate . . . . *Lindsaea*
b. Segments cuneate . . . . . *Sphenomeris* (or *Odontosoria*, sens. lat.)

It is evident that such a distinction, based on the shape of the ultimate segments only, does not look very natural, at any rate in a group with such diverse types of leaf-pattern as the Lindsaeoids, and several authors have commented on the difficulty to distinguish the two genera (notably HOLTTUM, 1947, p. 134/135). MAXON's distinction (1926, p. 392):

a. Rhizomes densely hairy . . . . (a.o.) *Sphenomeris*
b. Rhizomes paleaceous . . . . (a.o.) *Lindsaea*

is only true with regard to *S. clavata*, the only species included in his treatment, and even there the flattened structures that clothe the rhizome are occasionally two cells wide at the base; they are certainly not comparable to the true hairs on rhizomes of other fern-genera. Moreover, in most other species of *Sphenomeris* true scales are found. (It seems, however, that in later years Maxon himself became doubtful with regard to the validity of *Sphenomeris*; see p. 153).

During the author's studies of the neotropical species it soon became evident that none of the afore-mentioned distinctions between the two genera is of much value. The south-east Brazilian *Lindsaea virescens*, which has incised, yet clearly dimidiate pinnules, is closely related to the sympatric *L. bifida* which fits perfectly in the description of *Sphenomeris* (*Stenoloma*) of most authors, is keyed out to that genus in their keys and is usually included there (or in *Odontosoria* sens. lat.). Likewise, *L. meifolia*, also currently referred to *Odontosoria* or *Sphenomeris*, is very close to *L. pendula*; an intermediate between the two has been found which is almost certainly of hybrid origin (described in this paper as

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*) It seems superfluous to discuss again the application of the name *Stenoloma*, sometimes made to replace *Sphenomeris*, as this has already been done at great length. The interested reader may be referred to COPELAND (1947, p. 54) and PICHI-SERMOLLI (1954, p. 445). The necessity to conserve *Sphenomeris* against *Stenoloma*, as was done by the International Botanical Congress at Paris, 1954, is in the present author's opinion at least questionable.

L. × *dissecta*) *), and it seemed quite arbitrary to put the members of these pairs of species into different genera. Moreover, *L. bifida* and *L. meifolia* would be quite isolated among the bulk of species of *Sphenomeris*. Must we then conclude that *Lindsaea* and *Sphenomeris* cannot be seperated? The author was at first inclined to believe that this was the case. In this connection Pérez Arbeláez (1928) might be cited who went even further and included *Odontosoria* with *Sphenomeris* and "*Saccoloma*" *imrayanum* (removed by him on good grounds from that genus) all in *Lindsaea*. His taxonomic conclusions are, however, based on anatomical and morphological data taken from a few sample-species only. But he observed correctly that the shape of the ultimate divisions alone cannot be used to divide the Lindsaeoid ferns into satisfactory genera. Christensen's suggestion (1932, p. 77) to create a new genus between *Lindsaea* and *Sphenomeris* confronts us with the difficulty to draw two borderlines instead of one and therefore does not simplify the matter at all.

Subsequent studies of morphological details carried out by the present author showed, however, the presence of points of difference that can serve to distinguish the two genera. They may be summed up as follows:

	Sphenomeris	*Lindsaea*
rachis-ridges	continuous on both sides	interrupted on the acroscopic side
indusium	short, attached at the base and at least part of the sides	short, attached only at the base, or elongate
sporangia	large, over 300 μ long (exc. *S. clavata*), $>$ 14 indurated annulus-cells	smaller, rarely slightly over 200 μ long, mostly 9–14 indurated annulus-cells

The importance of the structure of the rachis for the taxonomy of ferns was fully recognized by Holttum (1947). In the Lindsaeoid ferns, the adaxial side of the axes is channelled, the channel bordered by ridges which, at least on the basiscopic side, are continueus with those of the axes of the next higher order and with the thickened edge of the leaflets. (There are a few exceptions to this rule, e.g. in *L. macraeana*, where the adaxial face of the petiole and rachis is raised beyond the point of insertion of the pinnules and not sulcate). In *Sphenomeris* and *Odontosoria* these ridges are continuous on both the acroscopic and the basiscopic side; in *Lindsaea* they are interrupted on the acroscopic side (in the "axil" of the junction.) In some species this interruption is not too well-marked (e.g. in *L. virescens*), but generally it can be observed.

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*) Hybridization in itself is not quite sufficient to warrant inclusion in one genus; there are a few examples of intergeneric hybrids in ferns, e.g. *Pleuroderris michleriana*, supposed to be *Dictyoxiphium panamense* × *Tectaria* (*rivalis*?). The hybrids *Camptosorus* × *Asplenium* and *Ceterach* × *Phyllitis* should not be taken as examples, as inclusion of all these genera in *Asplenium* is perhaps more natural.

The indusium of *Sphenomeris* (which has uni- to quadrinerval sori) is attached at the base and at least part of the sides; its base, particularly in short sori, tends to be convex, and in most species the sporangia do not strongly protrude at full maturity. In *Lindsaea*, on the other hand, the indusium of species with short (uni- or binerval) sori is attached at the base only, with tendency to be concave, more or less horseshoe-shaped. This is clearly observed in *L. bifida* and its relatives and in short sori of *L. virescens*. In species with long (coeno-) sori it is sometimes more or less attached at the sides, but these differ widely from *Sphenomeris* in other characters.

The sporangia of *Sphenomeris* are large, over 300 μ long and 200 μ wide, with the sole exception of *S. clavata*, where they are about 220 × 170 μ; their number per sorus is mostly small, which is particularly noticeable in uninerval sori. *Lindsaea* has smaller sporangia, most of them between 130 and 165 μ in length, in a few species (nos. 4, 5, 27, 28, 30, 33, 42, 43, 44) slightly over 200 μ long, but all these species are clearly Lindsaeas by the virtue of other characters. The number of sporangia is large in *Lindsaea*, even in uninerval sori. The shape of the spores cannot be used as a differential character, as monolete and trilete spores occur side by side both in *Lindsaea* and *Sphenomeris*.

An additional differentiating character is found in the rhizome scales. Those of *Sphenomeris* are either very long, in some species over 5 mm, and have a very long subulate apex of only one row of cells, or they are shorter, but retain the very long hair-like apex (e.g. in a form from São Tomé called *Stenoloma chinense* var. *divaricatum* (Christ) Alston by ALSTON 1944, p. 73, which probably represents a separate species), or all of them, not only the reduced ones, are of one row of cells throughout or practically throughout (e.g. in *S. clavata*). The scales of *Lindsaea* are ovate to narrowly lanceolate, up to 2 mm long (in a few cases longer, but then without a long subulate apex), the apex of one row of cells is comparatively short or wanting, and only the strongly reduced scales occurring together with the larger ones in many species are of one row of cells throughout (fig. 2, 4, 5).

We see, then, that although the architecture of the leaf and the shape of the ultimate divisions alone are not sufficient to separate *Lindsaea* and *Sphenomeris*, there are other characters that help to place species of doubtful alliance. There is a gap between *Sphenomeris* and *Lindsaea* that separates them clearly; from this, however, we must not conclude that it is easy to define them. Two of the characters mentioned above as typical for *Sphenomeris*—acroscopically not interrupted rachis-ridges and large sporangia—do occasionally occur to a certain extent in *Lindsaea*; and the small scales of some Lindsaeas are approached by those of certain species of *Sphenomeris*. In these cases, however, the combination of all other characters presents sufficient evidence to place these species in one of the two genera.

It has been possible to study most species referred to *Sphenomeris* (or "*Stenoloma*"). In the writer's opinion, the following species have their natural place in this genus:

S. alutacea (Mett.) Copel., New Caledonia.

S. chusana (L.) Copel., widespread in the tropics of the Eastern Hemisphere.

S. deltoidea (C, Chr.) Copel., New Caledonia and adjacent islands.

S. killipii (Maxon), Colombia.

S. melleri (Hook.) C. Chr., Madagascar.

S. retusa (Cav.) Maxon, Philippines, New Guinea, etc. (probably including *Odontosoria decipiens* (Cesati) Christ)

S. spathulata (Maxon), Colombia.

S. veitchii (Baker) C. Chr., North Borneo.

S. clavata (L.) Maxon, Florida, Bahamas, and Greater Antilles, the type species of the genus; it has smaller sporangia than any of the above-named species, and very narrow scales, shared only with *S. chusana*.

Stenoloma bifidum (Klf.) C. Chr., *S. decompositum* (Bak.) C. Chr. and *S. eberhardtii* (Christ) Ching constitute a group of closely related, very primitive species of *Lindsaea*, more fully discussed in connection with the first-named species and on p. 135.

It is not impossible that *Sphenomeris* is not a natural genus, but was developed along several distinct lines. In this connection it may be of interest that two types of sporangia are found in the genus. One possesses an annulus the indurated part of which touches the apex of the stalk of the sporangium and is there slightly oblique, a condition found throughout *Lindsaea* (fig. 21) (except in the section *Tropidolindsaea*, fig. 20) and in *Ormoloma* (fig. 19); in the other, the last indurated cell is separated from the stalk by one non-indurated cell. The first type was found in *S. alutacea*, *S. chusana* and *S. clavata*, the other in *S. retusa*, *S. melleri*, *S. spathulata*, *S. killipii*, and *S. deltoidea*, (fig. 18), but in some of these species the lowest indurated cell almost reaches the stalk, and the character is probably of comparatively little importance. A revision of *Sphenomeris*, preferably connected with one of the Old-World Lindsaeas, would be necessary to decide whether *Sphenomeris* is a natural entity or not. In such a revision, it would also be necessary to demonstrate in what way the strongly dissected forms of *Tapeinidium* (mostly from New Caledonia) can be separated from *Sphenomeris* in a satisfactory way; at present the writer is unable to suggest in what direction the solution should be sought.

5. The place in the system

The first species of *Lindsaea* were described in *Adiantum*, those of *Sphenomeris*, *Odontosoria*, as well as highly compound forms of *Lindsaea*, mostly in *Davallia*.

As mentioned before, many authors placed *Lindsaea* in the Davallioid (or Dicksonioid) ferns (in an inclusive sense, comprising also the genera centering around *Dennstaedtia*, now considered to form a special group), although sometimes in a group *Lindsaeae* etc. of lower rank; examples are Presl (1836), Hooker & Bauer (1842), J. Smith (1842), Mettenius (1856), Christ (1897), Diels (1902), van Alderwerelt van

Rosenburgh (1908), Sim (1915), Bower (1928), and Pérez Arbeláez (1928); by others it was classified as a separate tribe etc., all by itself, or associated with closely allied genera, some of which are now united with it, such as *Synaphlebium* J. Smith, *Isoloma* J. Smith and *Schizoloma* Gaud. As examples may be given Hooker (1844–46). Fée (1852), Moore (1857), Baker (1870, 1874), Kuhn (1882). In both cases, *Lindsaea* was usually followed in the system by *Adiantum*, which formed a group of its own or was the first genus of the *Pterideae*. But rarely was *Lindsaea* included in one group with *Adiantum*: Kaulfuss (1827).

Christensen (1938) definitely assigned the Lindsaeoid ferns to the rank of a subfamily of the *Polypodiaceae*. Here they appeared in the second place, after the *Dennstaedtioideae* and before the *Davallioideae*, thus in a position that indicated primitiveness. Ching (1940) raised them to family-rank in a similar position. Copeland (1947) included them in his *Pteridaceae* as a group of probably remote independent origin (p. 79). Holttum (1917, 1949) placed them in his *Dennstaedtiaceae* between the *Dennstaedtioideae* and the *Davallioideae*, which is in close agreement with Christensen's ideas. In the second publication cited, Holttum expressed some doubt on the naturalness of inclusion in the *Dennstaedtiaceae* and suggested they might perhaps better be put in a separate family of their own (p. 286), but he kept them in that family in 1954.

It appears to the author that at the present stage of our knowledge it would hardly be justified to recognize a family *Lindsaeaceae*. It is true that the alliance to the Dennstaedtioid ferns is not very close, and that to the Davallioids, which differ markedly by their mostly peltate scales, articulate stipes, and much more complicated vascular system of rhizome and stipe, is even less evident; but as long as we cannot conclude with reasonable certainty whether some supposedly primitive characters of the Lindsaeoids, particularly the very simple stele, are signs of true primitiveness or are due to reduction, it would be rash to remove them from the vicinity of these groups, which, at any rate, seem to be their closest relatives. It seems best to treat them as a subfamily; whether of the *Polypodiaceae* or of the *Dennstaedtiaceae* *) (which, in the author's opinion, are a more natural entity than Copeland's *Pteridaceae*) depends on the more modern or more conservative attitude one assumes in the classification of the leptosporangiate ferns; the author would at present prefer the second alternative.

6. Cytology

In recent years, cytological data have contributed very materially to clear up the taxonomy of species as well as larger groups of ferns. We owe most contributions in this field to the brilliant work of I. Manton. Unfortunately, in the case of the *Lindsaeoids*, the chromosome numbers do not furnish much new insight, neither for the delimitation of the genera nor for the establishment of the affinities of the whole group, although it must be admitted that so far they are known in a very small number of species only.

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*) For the name of this family, see Morton in Am. Fern Jo. 46:159 (1956).

The following data have been taken from Manton & Sledge (1954) and from Manton's appendix to Holttum (1954). The author is much indebted to Professor Manton for her permission to include some additional unpublished data which she was kind enough to communicate. All are from Old World species.

		origin	n
Lindsaea	caudata	Ceylon	82
	concinna	Australia	47
	cultrata	Ceylon	82
	,,	,,	± 150
	decomposita	Malaya	± 50
	,,	,,	± 100
	ensifolia (Schizoloma)	Ceylon	88
	nitida	Malaya	± 47
	parallelogramma	,,	47
	pectinata	,,	± 50 (47?)
	scandens f. terrestris	,,	± 47
Sphenomeris	chusana	Ceylon	± 100
	,,	Malaya	± 145–147

Although the majority of the species have about 50 as basic number, with which *Sphenomeris chusana* agrees, several do not seem to fit at all; these are morphologically not particularly distinct, except *L. ensifolia*. It is to be hoped that more data will be available before long, also of species from the Western Hemisphere. The supposed affinity to the Dennstaedtioid and Davallioid ferns has so far not been found to be reflected by the chromosome numbers; Dennstaedtioids: *Microlepia* n = 43, *Hypolepis* n = ca. 104, *Dennstaedtia* n = prob. 32; Davallioids: all n = 40.

7. Morphology and anatomy

The most detailed accounts on the anatomy and morphology of the Lindsaeoid ferns have been given by Bower (1923, 1928), Pérez Arbeláez (1928) and Wagner (1952 b.) The two last-named publications are in the following simply referred to as "Pérez Arbeláez" and "Wagner."

Some aspects of the morphology have already been dealt with in the preceding paragraphs and are not again discussed extensively. For details of the laminal morphology, the reader is referred to the next paragraph.

The observations on anatomical structures reported in this paragraph are based on sections of samples of such material as was readily available or particularly suitable. A complete survey of the anatomy of all species would, of course, fall outside the scope of the present revision. As it is quite possible that the results obtained from one or a few species are not generally applicable, especially as to details, the species from which they were taken are mentioned as a rule.

Most sections were prepared from herbarium specimens, as the author had no access to fresh material, except several wild plants of *L. stricta* which Dr. G. R. Proctor, Kingston, Jamaica, was kind enough to send, and a leaf of the Asiatic *L decomposita* from the greenhouses of Kew Gardens. That so little cultivated material has been available is due to the fact that Lindsaeoid ferns are hardly ever kept alive in greenhouses for a long time, especially species of *Lindsaea*, and their spores refuse to germinate. Herbarium specimens prepared from cultivated plants are exceedingly rare. KUNZE's statement (Linnaea 21: 229, 1848): "Qua ex causa Lindsayae culturae resistant, nescio. Sporae optimae notae . . . . nunquam germinarunt" still holds good. We do not know the reason.

All sections were prepared by hand, with so-called single-edge razor-blades on a substrate of soft wood. This method proved to yield good results in a very short time. Sections of leaves were mostly stained, either with safranin or with ferrichloride and tannic acid. Fragments of leaves were cleared in dilute KOH or NaClO, stained with the afore-mentioned agents, and mounted in glycerine-jelly. Sections of rhizomes and petioles were mounted in the same way without staining; these organs were softened before sectioning by short immersion in a solution of "Aerosol O.T." (a commercially available detergent) in distilled water and methyl-alcohol. The author is indebted to Dr. F. Meyer, St. Louis, Mo., for drawing his attention to this very useful agent. It also proved invaluable in preparing slides of rhizome-scales and sporangia; the rhizome or sorus was moistened with a few drops of "Aerosol"-solution, and scales or sporangia could be scraped off practically without any loss or breakage. Afterwards they were mounted in lactic acid which apparently did not have a swelling effect but made them somewhat more translucent, and ringed with ringing cement.

The author is very much indebted to Mrs. P. Y. de Leng–Doewes who prepared for him the majority of the sections.

a. The rhizome

The stele of most Lindsaeoid ferns is of a peculiar type, as yet not observed in adult rhizomes of any fern outside this group. It is known as the *Lindsaea*-type and was discovered by TANSLEY & LULHAM (1902). It was later commented on by BOWER (1923, p. 146/47; 1928, p. 31), PÉREZ ARBELÁEZ (p. 55/56), OGURA (1938, p. 52, 373), COPELAND (1947, p. 79), and others. It is essentially a protostele, but inside the xylem a strand of phloem is found (see BOWER, fig. 136 = fig. 600, fig. 137, PÉREZ ARBELÁEZ, fig. 24, etc.). This internal phloem is not accompanied by pith or by an endodermis, as is the case in a solenostele, although a small strand of these two tissues is present inside the internal phloem near the nodes (TANSLEY & LULHAM, l.c.). The internal phloem is usually situated towards the dorsal side of the rhizome (reported by the authors cited above; checked by the writer in *L. lancea*, *virescens*, *protensa*, and *Sphenomeris clavata*), but occasionally approximately central (in both species of *Ormoloma* where it is very large and occupies about one-half of the diameter of the stele). A true solenostele, with internal endodermis and pith, has been reported in some species of *Lindsaea* ("*Odontoloma*", Bower, 1923, p. 147), in *Odontosoria* (id. 1928, p. 31) and in some species of *Sphenomeris* (S. *retusa*, Bower, l.c.; *S. alutacea*, Pérez Arbeláez, p. 56).

The fact that the *Lindsaea*-type of stele is a kind of intermediate between protostele and solenostele and that it has been found in young stages of genera where in mature plants true solenosteles are found ("*Pteris aquilina*", "*Nephrodium molle*" and *Anemia phyllitidis*, Tansley & Lulham, l.c., p. 160) has induced several authors to regard it as a true intermediate, that is, from a phylogenetic viewpoint. These arguments seem to the present author to be by no means conclusive; the possibility that the *Lindsaea*-type is a reduced type of solenostele, already indicated by Copeland (l.c.), should be seriously considered. The relation between diameter and structure of the stele in different species found by Bower (1928, p. 31), i.e. stouter rhizomes having a solenostele, more slender ones a *Lindsaea*-stele, shows how careful we should be before assigning any phylogenetic significance to this character.

The xylem, consisting mainly of tracheids of rather variable diameter with scalariform pitting, is approximately circular in cross-section and is surrounded by a thin layer of phloem, the structure of which has not been examined more closely, as herbarium-material is hardly suitable for this purpose. On the outside of the phloem are the pericycle and the endodermis, which in their turn are surrounded by a few (3–4) layers of thin-walled, parenchymatous cortex-cells filled with starch-grains. These pass to the outside abruptly into a thick strong sheath of highly sclerenchymatous outer cortex consisting of about 10–15 layers of cells of rather variable diameter, the outer ones mostly smaller and somewhat less sclerified. All walls are strongly tinged with brown, and as a rule all cells contain starch-grains. This thickened cortex occupies 1/2 to 3/4 of the diameter of the rhizome, thus rendering it difficult to dissect; the layers between the thickened cortex and the xylem are usually crushed or torn in sectioning. The little differentiated peripheral layer of cells that constitutes the epidermis of the rhizome bears the scales. These are attached to a few cells along a short line which in very broad scales is surpassed by their lateral edges, giving them a subpeltate appearance (see also Pérez Arbeláez, fig. 23 j). The equal thickening of all walls of the scales can be well observed in cross-sections. For further notes on the scales, see pp. 105, 118.

The narrow, reduced scales are most numerous near the apex of the rhizome because they are more readily caducous than the broader ones; relatively few are found on older parts.

b. The root

The roots are attached to the ventral and lateral surfaces of the rhizome, sometimes close to the dorsal side. Pérez Arbeláez described them as arising in pairs below each leaf. Such a regular distribution was not observed by the present author; moreover, their number is often considerably larger than twice that of the leaves or leaf-bases. They are about 1/4–3/4 mm in diameter and ramify freely in their distal part in a non-dichotomous way. Root-hairs are present almost throughout.

In cross-sections (fig. 1) a simple protostele without internal phloem can be observed. The xylem consists of a few large and two groups of small tracheids (diarch), surrounded by phloem, a discontinuous layer of pericycle-cells, and the endodermis. The stele is approximately hexagonal in cross-section, as the innermost layer of cortex consists of six (or a few more) very large cells, the space between them being occupied by the stele; the outer layers of the cortex are formed by smaller and more highly sclerified cells. All cortex-cells contain starch (not indicated in the figure).

c. The petiole

The petioles are attached to the dorsal side of the rhizome. When they are remotely disposed, they are aranged in one row only, but where they are close together they often show a tendency to be more or less distichous. Their length varies with the size of the leaf; in small leaves they are relatively short, much shorter than the laminal part, but in large leaves they are much longer, often considerably longer than the blade. They are continuous with the rhizome, the xylem of which is broken at the nodes where inner and outer phloem come into contact; but true leaf-gaps are absent, as the phloem is unbroken (see TANSLEY & LULHAM, l.c., BOWER, l.c., etc.; not checked by the author.) The petiole is terete at the base, otherwise at least the adaxial surface is flattened or mostly sulcate. The abaxial side is terete, angular, or channelled, depending on the species. These angles or channels do not seem to appear as a result of drying as was suggested by WAGNER (p. 87), but represent the natural condition, as can be observed in fresh material and also in sections, where no shrivelled or collapsed cells are found adjacent to these structures. The description of the channels, ridges, etc., sometimes given in field-notes, is in close agreement with the condition observed in the dried specimens.

The stele of the petiole is approximately triangular in cross-section, rarely oblong (observed in *L. protensa*). The xylem is arranged in one deeply U- or V-shaped strand with the sinus on the adaxial side. The smallest elements occur at the bottom and on the outer sides of the arms; the xylem is apparently triarch. This kind of petiolar stele is called the *Loxsoma*-type. PÉREZ ARBELÁEZ figured the stele in the petiole of *Sphenomeris chusana* as consisting of two separate strands of xylem (fig. 24 1, as "*Lindsaya chinensis*"); but according to the present author's observations which were, however, carried out in other species, there is always a strand, sometimes very narrow, of small tracheids that links the two arms together at the base. The sinus of the xylem is filled with parenchymatous tissue. The phloem is most strongly developed towards the ends of the arms; it penetrates into the sinus for some distance and is only very weakly developed at the abaxial side of the bottom. There is a distinct pericycle of 1–3 layers of cells and an unbroken endodermis. The structure of the cortex is essentially the same as in the rhizome, but there are usually more layers of internal non-sclerotized cells, and the transition to the outer heavily thickened layers is mostly more gradual. The thickened walls are stramineous to dark brown, depending on the species, except at the extreme base of the stipe, where the cortex is always very dark. There are no traces of pneumathode-areas with soft, well-aerated tissue which were described from other ferns by Bower (1923, p. 169), Tindale (1956, p. 328), and others. The petiole is apparently devoid of stomata.

d. The rachis

There is no fundamental difference in anatomical structure between the petiole and the rachis. In primary and secondary rachises the same adaxial channels are found as on the petiole, and all are continuous with each other. The ridges bordering these channels are, at least in *Lindsaea*, almost always distinctly discontinuous on the acroscopic side of a node, whereas they are continuous on the basiscopic side, as has been described above. This condition prevails practically invariably at the insertion of the pinnules. The channel is continuous to the very apex of the rachis of the highest order where its sides pass into the thickened edges of the terminal segment or pinnule.

The abaxial side is more variable in structure; it may be terete, angular, channelled, or in a few species keeled; but at least in its apical part the rachis of the highest order is almost always grooved on the abaxial side. The ridges bordering this groove fuse towards the apex of the pinna (lamina) to form a keel, approximately at the point where the pinnules are confluent into the terminal segment, or in the base of the terminal pinnule in the species where this is present.

Fig. 1: Cross-section of a root of *Lindsaea stricta* var. *stricta* (Mexía 5486). Fig. 2: Rhizome-scale of *L. stricta* var. *stricta* (Fanshawe M 240). Fig. 3: Scale from very young leaf of the same species (Blanchet 2315). Fig. 4: Rhizome-scale of *L. filipendula* (v. Lützelburg 141). Fig. 5: Rhizome-scale of *L. seemannii* (Haught 5581). Fig. 6: Cross-section of secondary rachis of *L. divaricata*, showing membranous wings on the adaxial side and a pinnule-trace to the left of the main stele (Ll. Williams 14685). Fig. 7: Diagrammatic cross-section of primary rachis of *L. stricta* var. *parvula;* cross-hatched: stele; dotted: chlorophyll-containing inner cortex; vertical lines: sclerified outer cortex. Fig. 8: Cross-section of pinnule of *L. schomburgkii* f. *densa*, showing sclerotic tissue along vein and edge (Steyermark 59474). Fig. 9: Hairs from the dorsal epidermis of pinnule of *Sphenomeris melleri* (Lam & Meeuse 5349). Fig. 10: Dorsal epidermis of pinnule of *Lindsaea arcuata*, showing hair and stomata (Skutch 3737). Fig. 11: Dorsal side of apex of pinnule of *L. virescens*, showing receptacle, indusium, and marginal strand (sporangia omitted) (Hooker s.n.). Fig. 12: Ventral epidermis of segment of *L. bifida*, showing pattern of more elongate cells above the veins and its evanescence towards the distal side ((Mexía 4066). Fig. 13: Cross-section of rachis of *L. stricta* var. *stricta* near junction with secondary rachis, showing patch of dark, sclerified cortex between the steles ("axillary cushion") (Proctor s.n.).

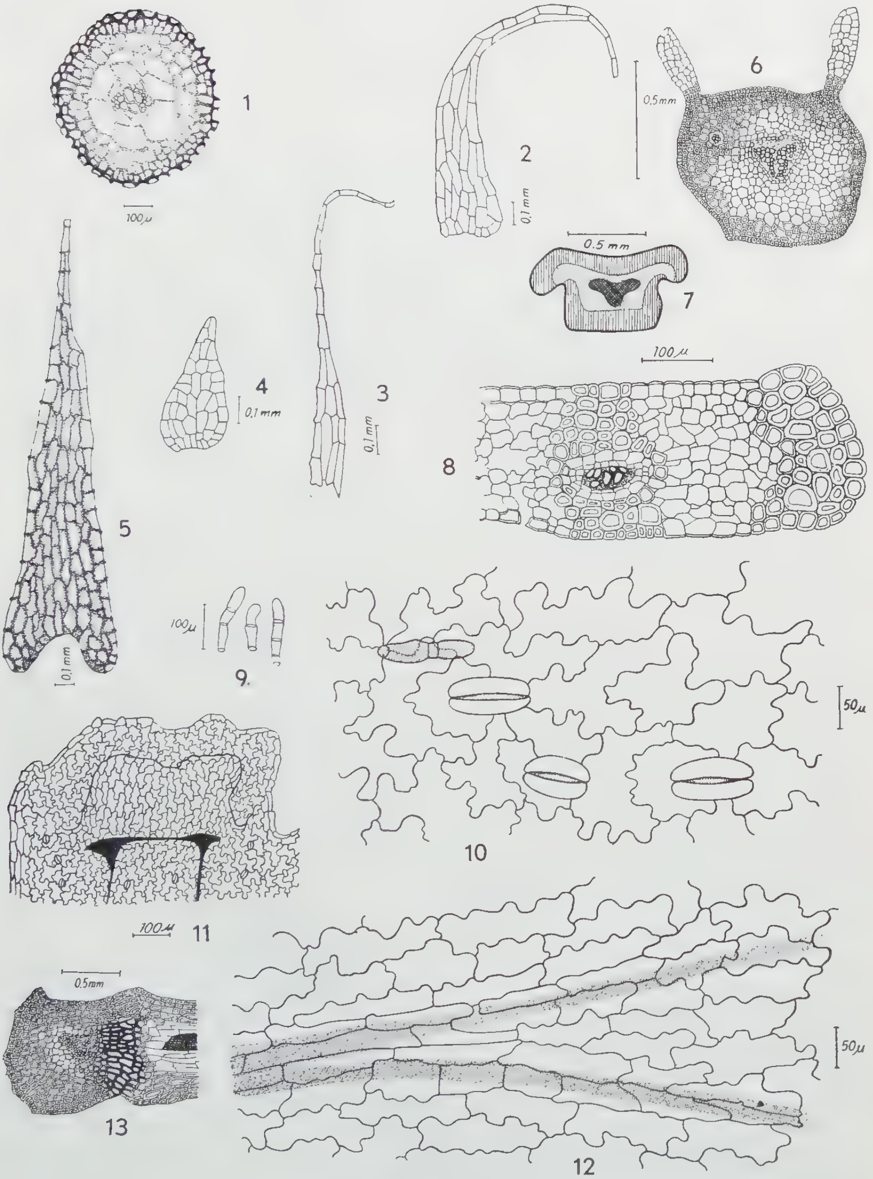
1
100μ
2
0,1 mm
0,5mm
6
0.5 mm
7
100μ
4
0,1 mm
3
0,1 mm
5
0,1 mm
8
100μ
9.
50μ
10
100μ
11
0.5mm
13
50μ
12

Fig. 1—13

The vascular bundle of the rachis becomes less deeply lobed as it decreases in size and the two arms of the xylem touch across the sinus, sometimes cutting off small areas of parenchyma. The vascular supply to the secondary rachises and the pinnules is given off from the apex of the arms; the daughter-strands run for a small distance outward under a small angle, then bend sharply to the side and leave the main axis.

The outer layers of the rachis cortex are again heavily sclerified, mostly with a gradual transition to the thin-walled inner layers (see fig. 6, 13). In recently collected specimens these thin-walled layers can be seen to contain chlorophyll; this may be universally present, but probably disappears through discoloration in older material. Starch-grains are often present in addition. The walls of the thickened layers are often tinged with brown; this colour may prevail on the adaxial side (*L. stricta*), on the abaxial side (the Asiatic *L .decomposita*) or may be evenly distributed (e.g. *L. hemiptera*). The presence and distribution of this colouring matter is sometimes characteristic for the species.

On the edges of the rachises (and of the upper part of the petiole) membranous, more or less wing-like outgrowths are sometimes present. They prove to have a taxonomic importance which has thus far hardly been recognized. They are as a rule less sclerified than the rachis itself and are never tinged with brown; consequently, when the rachis itself is dark, they contrast sharply. They are found on the adaxial side of the rachises in *L. hemiptera*, on the adaxial side of the primary and on both sides of the secondary rachises in *L. divaricata*, and on the four sides of all rachises in *L. tetraptera*. In the latter species they are rather thick and taper gradually to the edge; in the two others they are of approximately constant thickness (fig. 6). Their function seems to be unknown. They definitely do not represent aerating tissue; their internal structure is not less compact than that of the cortex, although they are less sclerified. No stomata have been observed on them; moreover, in *L. divaricata* and *L. hemiptera* they are cut off from the loose inner layers of the rachis by a continuous layer of sclerotic tissue at their bases.

A structure which probably serves aerating purposes was found in *L. stricta* var. *parvula*. Here the adaxial side of the primary and secondary rachis, usually also of the upper part of the petiole, is at least in some places considerably broadened and projects beyond the abaxial portion; it is visible from the adaxial side as a ledge. This, incidentally, is the main characteristic feature of var. *parvula*. In cross-section the axis has roughly the shape of a felt hat, with the rim on the adaxial side (fig. 7). The inner layers of the cortex consist of thin-walled cells containing chlorophyll. This zone of green cells extends into the "rim" of the "hat". On the groove that separates the "rim" from the main body the sclerotic tissue that surrounds the green layer in other places is absent, and the latter almost reaches the surface. The epidermis is strongly wrinkled in this place; here one stoma was observed by the writer. It is possible that this structure represents a special adaptation to the swampy habitat with badly aerated subsoil in which *L. stricta* var. *parvula* is usually found.

A structure that to the author's knowledge has not been described so far is found in many (perhaps most or even all) species. On the abaxial side of the primary rachis in at least bipinnate leaves at the junction with a secondary rachis an oblong or cuneate swelling is found which in species with pale rachises is often darker, in species with very dark axes sometimes paler. It is particularly conspicuous in *L. cultriformis* and *L. divaricata*. Under the binocular microscope the epidermal cells can be seen to be larger and approximately round, whereas elsewhere on the axes they are quite elongate. In the taxonomic part of this paper these structures are referred to as "axillary cushions".

Their internal structure could be studied in one instance, namely, in fresh material of *L. stricta* var. *stricta* from Jamaica. In this material in a cross-section of the primary rachis at a node a large group of cortical cells was observed, mostly belonging to the inner layers with larger diameters, which were strongly tinged with brown and appeared to be somewhat more sclerified than the surrounding cells. This tissue extended to the abaxial surface and almost reached the stele of the primary rachis which it surrounded for about one-third of its circumference (fig. 13). The sections did not show whether it also extended to the stele of the secondary rachis. Similar but less extensive structures were found at the point of attachment of the pinnules; they were observed in the same material, and in a fresh leaf of the Asiatic species *L. decomposita*. The large brown cells appeared as a plate in cross-section, situated between the main and the tributary stele, but closer to the latter. From the outside these groups of cells near the base of the pinnules are not visible but it is quite possible that they are found in all species with compound leaves. In cleared material they appear as triangular patches extending from the axil of the junction some distance downwards, keeping clear of both vascular bundles.

We can only make a guess about the function of these cells. It seems likely that they have a mechanical function, possibly strengthening the point of junction in order to prevent splitting off of the divisions of higher order that in most species come off under a rather small angle (at least rachises of higher order). Perhaps the larger lumina of these cells also play a role as aerating tissue, but so far no evidence for permeability to air from the outside has been found.

Externally similar, probably analogous structures can be observed on the axes of *Odontosoria* spp., notably *O. aculeata*.

e. The laminal parts

The lamina is practically always anadromic in the more than once pinnate Lindsaeoid ferns, the only ones where this character can be observed. The basal pinnule or secondary pinna is inserted on the acroscopic side of the secondary rachis. The basal pinnule is often strongly reduced and cuneate, especially if it is inserted very close to the junction with the rachis of next higher order, almost in the axil ("axillary pinnule") (fig. 23, 52). It is occasionally wanting; then the leaf is catadromic, but this is exceptional and never regularly found in any species. In addition to the basal pinnule, a few additional lower ones may be more or less reduced, sometimes only on the acroscopic side. The different types of pinnules and leaves of juvenile plants in terms of their general shape are discussed in the next paragraph.

In spite of their very diverse shape, the anatomy of the ultimate segments is rather uniform. A thickened strand of elongate, sclerotic cells runs along the margin. It is particularly well developed in the basal part of the basiscopic margin where it is continuous with the borders of the adaxial groove of the rachis, but it is present throughout the whole margin, although in some species, especially in those preferring dry or exposed habitats, it is much better developed and more conspicuous than in others; in *Lindsaea virescens*, for instance, it is almost absent, consisting only of one or two marginal rows of elongate, hardly thickened cells. Here the distal (apical) edge of the ultimate segments is minutely and irregularly erose; the smaller irregularities are due to certain cells of the marginal strand which project like papillae beyond the edge (fig. 11). A very obscure marginal strand is, however, uncommon. Comparable strands of sclerified cells extend along the bases of the veins in most species. The strand accompanying the main vein is as a rule united with the marginal strand of the lower edge of the pinnule for a certain distance. In a few species the sclerotic cells run along the greater part of or the whole of the veins which are elevated in dry specimens, as the leaf-tissue between them collapses in desiccation which is impossible for the sclerified tissue around the veins. In fresh material the veins are presumably immersed. Examples are *L. schomburgkii*, *L. semilunata*, *L. rigidiuscula*. The sclerotic tissue is most strongly developed on the dorsal and ventral sides of the bundles, especially the latter; laterally it consists of one layer of but weakly sclerified cells only and therefore hardly deserves to be called a sheath (fig. 8). Where it does not extend along the whole of the veins, it gradually tapers off in their distal part.

Comparable mechanical cells accompanying the veins have been described by Wylie (1948) from the dorsal epidermis of *Adiantum*.

The epidermis of *Lindsaea*, *Sphenomeris*, and *Ormoloma* consists of cells of very irregular outline that fit into each other like pieces of a jig-saw puzzle (fig. 10, 11, 12). On the ventral (adaxial) side where they overly the veins they are more regular in shape with much less wavy walls, and sometimes also more elongate. This condition gradually disappears in the distal parts of the veins (fig. 12), but reappears above their broadened ends in sterile pinnules. All epidermal cells contain chlorophyll; this is even the case in at least some of the thickened cells of the marginal strand. The cuticle is slightly thickened, more strongly in species from exposed habitats (*L. stricta*, L. *schomburgkii*, etc.). Stomata occur more or less in groups together between the veins, in *Sphenomeris clavata* in a few rows along the veins; in most species they are not at all numerous. The stomatal apparatus is surrounded by 2–6 epidermal cells (fig. 10). The stomata are restricted to the dorsal (abaxial) surface; otherwise no differences between the epidermis of the dorsal and ventral surfaces has been found, except for the cells overlying the veins described above. The author has not investigated possible differences in epidermis-pattern between different species such as have been found, for instance, by WAGNER (1954 a) in *Asplenium*. It seems that such differences are present at least in some cases, but only as slight variations of the same pattern.

Below the epidermis on the ventral (adaxial) side one or two layers of compact tissue analogous to palisade parenchyma but with approximately isodiametric cells are found; these and the ventral epidermis contain more chlorophyll than the rest of the leaf-tissue. This results in a darker shade of green on the adaxial surface of most species. The mesophyll is a very loose tissue of cells which have projecting arms; they appear to be round or oval (or rather irregular in sections prepared from dried material) in cross-section and more or less star-shaped in optical section in entire cleared pinnules. They are in contact with each other at the ends of their branches, leaving large open spaces between them. Small air cavities are found below the stomata.

The veins are evenly forked, but the angles they form with the vein from which they stem are often not quite equal, in connection with the oblique venation, especially towards the apex of the pinnules. They consist mainly of elongate tracheids with scalariform pitting and are enclosed in a sheath of elongate mesophyll cells visible in cleared material, some of which may be sclerified, as described above. In sterile pinnules they end in the tissue, well within the margin, and are broadened at their ends where the number of tracheids lying side by side is considerably increased; these tracheids are short and broad ("storage tracheids"). No hydathodes have been found at the ends of the veins, neither in sections nor in cleared and stained material.

f. Dermal appendages

Formerly the Lindsaeoid ferns were described as glabrous. But WAGNER (1952 b, p. 111/113) drew attention to the presence of two-celled glandular hairs in *Lindsaea*, *Sphenomeris*, and *Isoloma*. The present author is indebted to him for the communication of the best method to render these hairs visible. With the naked eye or a hand-lens they cannot be observed except in a few species of *Odontosoria. Notably* in *O. uncinella* and *O. jenmanii*, sometimes also in *O. gymnogrammoides*, a thin cover of hairs can be seen on the primary and secondary rachises near their junction. This was not mentioned by MAXON (1913), but observed in the first-named species by KUNZE (1851). This, however, is quite exceptional, and even under the microscope they are very hard to detect in unstained material, although they sometimes contrast by their yellowish colour. Staining with safranin renders them more readily visible, but the best contrast is obtained when cleared leaf-fragments or sections are stained with ferrichloride and tannic acid. According to WAGNER (in litt.) they are most readily found in young yet fully expanded leaves, especially on the abaxial surface along the veins and proximal to the sori. This can be fully confirmed by the writer. WAGNER (l.c.) reported them from *Sphenomeris clavata*, *Isoloma jamesonioides*, and four species of *Lindsaea* (3 Asiatic ones and *L. stricta*, called by him *L. guianensis*). To these the author can add *Sphenomeris melleri* (Madagascar), *Ormoloma imrayanum*, *O. standleyi*, *Lindsaea arcuata* (fig. 10), *L. bifida*, *L. guianensis ssp. lanceastrum*, *L. klotzschiana*, *L. parkeri*, *L. pendula*, *L. portoricensis*, *L. protensa*, and *L. quadrangularis* ssp. *antillensis*, that is, practically all species where they were sought after, and in species from almost all American sections. In none of the species was the absence of trichomes definitely established; it is quite likely that they occur throughout the group. They are usually two-celled, as stated by Wagner, and about 0.10–0.15 mm long, but three- or even four-celled ones (e.g. in *Sphenomeris melleri*, fig. 9), do occasionally occur.

Very young leaves are clothed with scales similar to those of the rhizome but narrower (fig. 2, 3). They are shed at a very early stage, as soon as the leaf begins to elongate, and are persistent only on the extreme base of the stipe.

g. The sorus and related structures

The sori are borne terminally on the veins the ends of which are considerably broadened, with short, wide tracheids. In species with uninerval sori the sporangia are borne on the broadened apex of the veins; otherwise there is a vascular commissure that also consists of rather short and wide elements (see BOWER, 1928, fig. 602.). This commissure usually extends laterally beyond the outermost veinlets which bear it, especially in species with long sori. In species with short sori and in incompletely fertile pinnules of species with continuous sori the commissures are usually present between the veins stemming from an ultimate or penultimate bifurcation, but this is no absolute rule, and at the base or apex of a pinnule one vein or a pair of veins is not rarely seen to be left out of the sorus (see BOWER, 1928, fig. 601). In species with short sori the sporangia may sometimes not be restricted to the end of a vein but may slightly extend along its distal part. The indusium is then somewhat oblique and approaches the situation found in the Asplenioid genus (or subgenus) *Loxoscaphe*. This condition is regularly observed in *Lindsaea millefolium* and *L. eberhardtii* (see p. 135); a somewhat different condition prevails in *Ormoloma* where the apex of the vein is sometimes extended parallel to the margin of the pinna; the indusium is then, of course, not oblique.

The vascular tissue of the receptacle does not reach the ventral surface (fig. 14, 15). The part of the lamina that extends beyond the receptacle, sometimes called the upper indusium, is similar in structure to the rest of the lamina but is devoid of veins and often also of stomata; these have, however, been found to be present in this part of the pinnule in *L. guianensis* ssp. *lanceastrum*, *L. klotzschiana*, *L. pendula*, *L.*

portoricensis, and *L. stricta*. This "upper indusium" consists in its outer part mostly only of the two epidermal layers which touch at their inner side; stomata, if they are present, are restricted to the proximal part where mesophyll is found between them. This part of the lamina is often set off from the remainder by a shallow groove on the adaxial side along the receptacle which may be visible to the nake eye, e.g. often in *L. portoricensis*. The edge of the "upper indusium" is formed by the sclerotic strand already described.

The indusium is attached along the proximal side of the receptacle (fig. 14). Laterally its attachment exceeds the extension of the receptacle. In species of *Lindsaea* with short sori and in *Ormoloma* it is attached by its base only; in species with longer sori the sides, too, may be more or less adnate, but they often taper considerably and it is then difficult to decide whether only the base or also part of the sides are attached. In *Sphenomeris* at least part of the sides are adnate to the epidermis.

At its base the indusium consists of several layers of cells, in its outer part of one layer only, or the latter condition prevails almost throughout, depending on the species. The outer edge is formed by a thickened strand similar to that of the laminal margin but much less developed. The cells are comparable to the epidermal cells of the lamina but tend to be more regular in shape and more elongate in a direction at right angles to the edge, except the marginal strand (fig. 11). In most species the indusium is reflexed at full maturity, apparently pushed aside by the bulging, dehiscing heads of the sporangia, but it seems that it becomes fixed in this position as it remains reflexed in cross-sections where the heads of the sporangia are almost always lost in sectioning. There is perhaps an active process involved that acts through the epidermal cells at the attachment of the indusium, pushing it back when the sporangia approach maturity.

The sporangia occur in several rows on the receptacle. BOWER (1928, p. 32/33) found them to originate in an initially gradate sequence that passed into a mixed state in *L. linearis*. The present author's material was not adequate to furnish additional data on this subject. They are long-stalked, the slender stalk consisting of about 4–7 stories of cells; at the base each story is formed by one or two cells only, in the upper part by three, and the cells of different stories may overlap considerably. The uppermost group of three cells is short and broad and forms a kind of pedestal for the head of the sporangium (fig. 15, 20, etc.). Paraphyses are frequently found intermingled with the sporangia; they resemble the trichomes of the vegetative parts. The autor found them in *L. cultriformis*, *L. dubia* (fig. 15), *L. hemiglossa*, *L. hemiptera*, *L. javitensis*, *L. lancea*, *L. quadrangularis* ssp. *terminalis*, *L. spruceana*, *L. stricta*, and *L. surinamensis*, but it is not unlikely that they are generally present. In ordinary slides prepared by scraping the sporangia off the receptacle with a flattened needle paraphyses are mostly not found; they are best observed when also pieces of the receptacle are scraped off, in sections, or in cleared and stained material. They are usually about 70 μ long and consist of two cells. WAGNER (1952 b, fig. 30) figured three-celled paraphyses in

L. stricta (as *guianensis*) and in *Sphenomeris chusana*; but the one figured by him in fig. 30 q may have been a sporangium the development of which was arrested at a young stage. The present author found large, up to 9-celled, paraphyses in *Sphenomeris melleri* (fig. 16), where they are so numerous and conspicuous that they are already visible under a binocular microscope. The strange forked or club-shaped paraphyses found by Kunze in *L. reniformis* (1840, p. 32; t. 16 fig. 2) have not been observed by the writer.

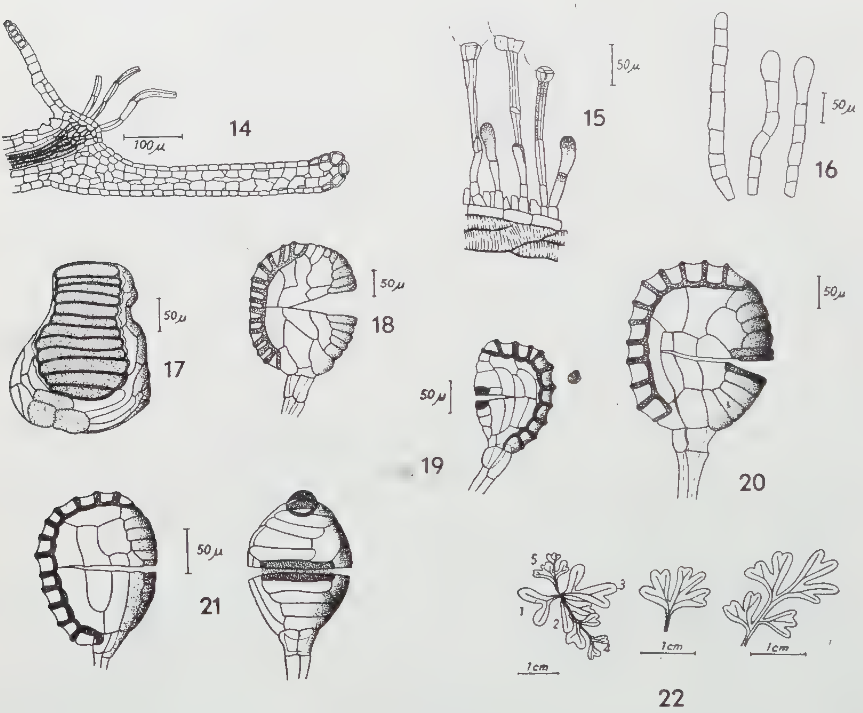

Fig. 14: Cross-section of edge of pinnule with sorus of *Lindsaea lancea* var. *lancea;* heads of sporangia detached (Krukoff 11264). Fig. 15: Receptacle, paraphyses and sporangia (without heads) of *L. dubia* (Steyermark 74684). Fig. 16: Paraphyses of *Sphenomeris melleri* (Lam & Meeuse 5349). Fig. 17: Sporangium of *Odontosoria aculeata*, showing oblique annulus at the point of insertion of the stalk (Valeur 291). Fig. 18: Sporangium of *Sphenomeris deltoidea* (Franc 358). Fig. 19: Sporangium of *Ormoloma standleyi* (Brade s.n.). Fig. 20: Sporangium of *Lindsaea seemannii* (Lehmann 737). Fig. 21: Front and side view of sporangium of *L. stricta* var. *jamesoniiformis* (Maguire & Fanshawe 23159). Fig. 22: Young sporeling and detached leaves of slightly older sporeling of *L. cultrata;* leaves of plant at left numbered in sequence, no. 5 not quite expanded (Kew Gardens).

The head of the sporangium is broadly elliptic, not more than about 1 1/2 × as long as wide, often less. The annulus tends to be slightly oblique, especially towards the base (see fig. 17), but is mostly interrupted at the stalk; it is continuous or almost so in the species of the section *Tropidolindsaea* (fig. 20). The indurated part is always strongly interrupted and never extends along the insertion of the stalk. The number of indurated cells is usually between 9 and 14, the number in one species mostly not varying by more than 4 or 5. A stomium is always present; it consists usually of 2 or 3 narrow transversely elongate cells, but 4-, even 5- or 6-celled stomia are sometimes met with in the same sorus as 2- or 3-celled ones. The slit occurs between the stomial cells but was in a few instances observed to be situated below them. The sporangia are mostly largest in those species of *Lindsaea* which occur in open habitats. This phenomenon is not found in *Sphenomeris* where all species have large or very large sporangia, whether they inhabit open localities (*S. alutacea*, *S. chusana*, *S. clavata*) or forests (*S. killipii*, *S. melleri*). The sporangia of *Ormoloma* (fig. 19) are very similar to the type commonest in *Lindsaea*, but the lowest indurated annulus-cell usually reaches to the middle of the uppermost stalk-cell and the interruption of the annulus is only very short. In *Sphenomeris* the structure of the sporangium is rather variable (see also p. 106); in some species they are very much like those of *Lindsaea*, e.g. in *S. clavata*, in others, especially in *S. alutacea* and *S. deltoidea*, the distinction between the indurated and the non-indurated part of the annulus is rather weak. The stomium-cells in these species are hardly or not more indurated than the adjacent cells, although they are laterally more elongate, and the edge of the sporangium opposite the indurated part of the annulus consists of an almost equal series of flat, elongate, stomium-like cells (see fig. 18). The spores of *Lindsaea* are with few exceptions smooth; they are minutely tuberculate in the Asiatic *L. eberhardtii*, not muricate, as stated by TARDIEU-BLOT & CHRISTENSEN (1939); see also WAGNER's illustration of the spores of *L. ensifolia* (1952 b, pl. 5 b). A perispore is always wanting. In most species of *Lindsaea* the spores are trilete; in most species from exposed habitats they are semiglobose, rather strongly coloured and rather large, whereas forest-inhabiting species mostly have deeply lobed tetrahedral spores which have probably collapsed; they are pale or hyaline and rather small. In *Sphenomeris* monolete and trilete spores are more evenly distributed; they are all large and strongly coloured, not collapsing. In the few American species of *Lindsaea* with monolete spores (*L. cubensis*, *cyclophylla*, *L. macrophylla*, *L. pallida*, *L. quadrangularis* ssp. *quadrangularis*, and the three species of the section *Tropidolindsaea*) these are flattened-elliptic or bean-shaped and hyaline or pale brown.

The taxonomic value of the spore-shape is not high but varies with the groups. In one subspecies of *L. quadrangularis* they are monolete, in the three others trilete; even if the treatment of these forms as subspecies of one species is proved to be unnatural, they are certainly closely related. *L. ensifolia*, rather closely allied to *L. macrophylla* with monolete spores, has trilete ones. *L. cyclophylla* is very close to *L. reniformis*, the spore-shape being one of the few diagnostic characters. On the other hand, the isolated position of the section *Tropidolindsaea* is stressed by the invariably monolete shape of their spores. There are a few other genera of ferns, e.g. *Vittaria*, where spore-shape is likewise not constant.

It has not been possible to make exact counts of the number of spores per sporangium. In some slides unopened, sufficiently translucent sporangia were present to permit close estimates. In some species the number was found to be probably 16, while in others it was definitely higher, but not much more than about 30. In this case it may be assumed that it is essentially 32, although it may be slightly smaller through abortion of one or two sporemothercells. In the special part, spore-numbers that were approximately established in this way are given as 16? and 32? respectively. BOWER (1928) gave the spore-number in *Lindsaea* as 16 or 32.

8. EVOLUTIONARY TRENDS

The Lindsaeoid ferns possess a number of characters that with justification may be considered as primitive, which has been the motive for regarding them as one of the most primitive groups of *Polypodiaceae* sens. lat. or of such families as have been split off from them. The creeping, radially symmetric rhizome of very simple structure and without leaf-gaps, the simple vascular supply of the stipe, the unspecialized scales may be interpreted as such. It is, however, open to doubt whether the Lindsaeoid stele in itself is evidence of primitiveness as opposed to the solenostele found in some representatives of the same group; it was supposed to be a transition between a true protostele and a siphonostele by Tansley & Lulham, Bower, and others. This has been discussed more fully in the preceding paragraph. Another point the author wishes to stress is that in his opinion the reduced rhizome-scales of many Lindsaeoids cannot be interpreted as transitions between hairs and scales as has been done on several occasions. The reduced ramenta called "hairs" or "bristles" are flattened, not cylindrical or moniliform, their cells are exactly like those of the true scales that mostly accompany them, and in species where the "bristles" prevail, undisputable scales with at least two rows of cells at the base are found sparsely intermingled with them (*Sphenomeris clavata* and *chusana*). They are quite different from the trichomes with presumably glandular function found on the foliar parts as was already pointed out by WAGNER (1952 b, p. 80). These hairs are perhaps reduced, and it is not impossible that the Lindsaeoid ferns stem from ancestors which had a more liberal indument of both hairs and scales; they may, at any rate, not be looked upon as a group where the transition from hairs to scales is taking place, so to speak, under our eyes. Generally the importance of the presence of hairs versus scales seems to have been somewhat overstressed in morphological and phylogenetic discourses on leptosporangiate ferns.

The uninerval submarginal sorus borne on the end of the vein present in *Tapeinidium*, *Odontosoria*, *Ormoloma*, and certain species of *Sphenomeris* and *Lindsaea*, is in all probability a primitive structure. But in *Sphenomeris* and—to a much greater extent—in *Lindsaea* we find along with it sori borne on an intramarginal commissure, culminating in the coenosorus with a receptacle uniting all vein-ends of a pinnule. This point is discussed more extensively below.

In this connection BOWER's findings with regard to the development of the sorus in *Lindseae linearis* should be mentioned. He reported (1928, p. 33, fig. 603) that "the receptacle arises from the actual margin of the blade into which the marginal segmentation is directly continuous, the indusial flaps arising as superficial outgrowths. The upper is stronger from the first, and elongates into the false margin of the blade, while the receptacle is tilted slightly towards the more delicate indusium." This is of great importance from a viewpoint of comparative morphology, but as the "false margin" exhibits the same structure as the rest of the blade, apart from the absence of veins and sometimes of stomata, whereas the "lower indusium" is much simpler, the sori may for practical purposes, when the mature condition is described, be called intramarginal and dorsal.

The slightly oblique, sometimes hardly or only shortly interrupted annulus (though always with strongly interrupted indurated part) is further evidence of primitiveness. On the other hand, the small number of spores in the sporangia (in *Lindsaea* probably 16 or 32) and the small number of sporangia per sorus in many species of *Sphenomeris* is an advanced character. Finally the venation, with dichotomous free or less often anastomosing veins (but always without included veinlets) is very probably a primitive feature. A midrib is almost always absent; the main vein, if there is one, is flexuose, suggesting sympodial origin.

The lamina

In few fern-genera such a great diversity of leaf-pattern is found as in *Lindsaea*. Here MARTENS & GALEOTTI's dictum ". . . cette belle famille des Fougères, où la nature a déployé dans le feuillage un luxe de formes que l'on ne rencontre dans aucune autre famille de plantes d'un ordre plus élevé" (1842, p. 3) is almost equally true within one genus.

As a result of his studies the author arrived at certain conclusions with regard to primitive versus derived types of leaves and the ways in which they are connected. In order to facilitate the understanding of the following pages, these conclusions are summed up in a scheme, where primitive characters appear at the beginning, derived ones at the end of each series.

Lamina: decompound—bipinnate (subtripinnate) *cum impari*—simply pinnate (with reduced confluent upper pinnules)—simply pinnate (with large terminal pinnule)—simple.
Pinnules (segments): cuneate, more or less divaricately furcate—dimidiate, incised—dimidiate, entire—hardly dimidiate, with an equal-sided apex.
Sori: uninerval—bi-plurinerval, discontinuous—continuous.

As far as other characters are concerned, monolete spores are probably derived, trilete ones primitive. The width of the indusium seems to be of little phylogenetic significance, but very narrow indusia are probably more derived.

The highly dissected leaf-type met with in *Odontosoria*, *Sphenomeris*, and some species of *Tapeinidium* and *Lindsaea*, with cuneate or linear ultimate segments and decompound architecture, should be looked upon as the most primitive. This opinion is shared by other Pteridologists, especially by HOLTTUM (1947), who believed this to be true also in other groups of ferns, notably in the Asplenioid, Blechnoid, and Lomariopsidoid ferns. It can hardly be denied that the highly compound leaf-type in the Lindsaeoids, if any, links them with their supposed relatives, the Dennstaedtioid and possibly also the Davallioid group, whereas the more condensed types, especially those with dimidiate pinnules, are not comparable to anything found in those groups, although analogous types are met with in much more remotely related genera (see below). Finally, phytogeographical data are in favour of this view. HOLTTUM (l.c.) regarded *Odontosoria* as the most primitive *Lindsaeoid*, but in the writer's opinion it seems more likely that the scandent, often spiny leaves with indefinite growth and subopposite primary pinnae of that genus arose as a specialization. It is difficult to decide whether *Sphenomeris* or the decompound group in *Lindsaea* is more primitive; *Sphenomeris* is perhaps more diverse, and if it can be shown to be polyphyletic, the evidence would be in favour of *Lindsaea* as the basic genus, a possibility pronounced by COPELAND (1947, p. 54). A further possibility would be the derivation of all these genera from an extinct parental form.

The leaf-type with dimidiate pinnules, the commonest in *Lindsaea*, is apparently derived from the previous type, largely through simplification. If on the penultimate division of a leaf of the first (decompound) type the number of ultimate divisions is strongly reduced, the only that are left are, for instance, a large acroscopic, perhaps forked, basal segment (because of the anadromic pattern of dissection found throughout the Lindsaeoids the first segment is always found on the acroscopic side), a smaller basiscopic and a still smaller apical one, this again more strongly developed on the acroscopic side. This is what is actually observed in the upper, reduced primary pinnae of e.g. *L. bifida* (fig. 36). If we turn to still more reduced pinnae above them, we see the basiscopic segment shift to a terminal position, pushing the apical segment to the acroscopic side. No segments are left on the basiscopic side, and the pinna looks rather like a dimidiate, but dissected pinnule of, e.g., *L. virescens* (fig. 34). Thus, together with the shifting of the basiscopic segment to the apex for which no "explanation" can be offered here, simplification (that is, reduction of the number of segments and also of their complexity) is the only process required to produce a dimidiate leaflet from a more highly dissected, merely anadromic, non-dimidiate one. This, of course, does not mean that simplification in such a case always results in the formation of a dimidiate pinnule. Yet strong arguments in favour of the concept developed above are found in some other genera. In *Odontosoria* there is only one species with ultimate segments that approach the dimidiate type, namely *O. uncinella*, which is the least compound species of the genus. Here, too, we see the transition from more highly dissected segments with approximately cuneate or flabellate lobes to dimidiate leaflets in the apex of the pinnae (fig. 25). The analogy with what is observed in *Adiantum* is discussed more at length in the next paragraph.

Together with the process that leads to dimidiateness we observe a tendency towards fusion of the segments which in turn creates the opportunity for the sori to fuse, as two or more vein-ends are found side by side in one ultimate segment, not separated by an incision. In *L. bifida* the sori are uni- or less often binerval, those of *L. virescens* are mostly bi- to quadrinerval. The process of the fusion is also met with quite independent from that leading to dimidiateness in *Sphenomeris* where certain species have strictly uninerval sori (*S. killipii*, *S. spathulata*) and others have broader segments with bi- to quadrinerval sori (*S. alutacea*, *S. retusa*, etc.).

The next step is taken when the webbing of the segments proceeds further, resulting in but shallowly incised pinnules which are found, for instance, in *L. klotzschiana* (fig. 45) and *L. cultriformis* (fig. 37), generally in the section *Temnolindsaea*. It is significant that in these species the edges of the lobes, and thus the sori, are not lying in one line in each other's prolongation, but are part of different lines intersecting at small angles with their neighbours (fig. 37). This apparently shows that they originated through condensation from more highly dissected types with ± divaricate segments and are not derived from forms with entire pinnules, through secondary occurrence of incisions.

Leaves of sporelings of the Asiatic *L. cultrata* were observed in the greenhouses of Kew Gardens; they are shown in fig. 22 and are somewhat different from those figured by WAGNER (1952 b, fig. 18 a). The webbing of the pinnule-segments observed on the mature plant which has only very shallowly incised pinnules is present here to a much lesser degree, which would be in accordance with the ideas expressed above if it is true that juvenile plants retain certain primitive characters not found in mature plants; but this is questionable.

PÉREZ ARBELÁEZ vaguely indicated a rather similar line of development (l.c., p. 88/89, fig. 34 a—f.) He was, however, inclined to read the sequence conversely as is done here. The assumption of the dimidiate type as basal seems to the present author to be untenable. It is morphologically isolated, and is certainly more specialized than the cuneately dissected type.

An interesting phenomenon is the simplification of the gross leaf-pattern that goes hand in hand with the webbing of the leaflets. The highly incised types, *L. bifida* and *L. virescens*, are decompound, but the species of the section *Temnolindsaea*, their closest relatives outside their own section, *Pseudosphenomeris*, are bipinnate *cum impari* (some of them occasionally even simply pinnate), that is, with a terminal pinna conform to the lateral ones. In some species of *Temnolindsaea*, notably in *L. klotzschiana*, but also in a few others from sections with continuous sori, the basal pinnules of the terminal pinna are sometimes larger, in *L. klotzschiana* often more deeply incised, which has probably to be interpreted as an obscure relict of decompound architecture. Also, the rachis of the terminal pinna shows by its structure that it is a prolongation of the primary rachis and not homologous to the lateral secondary rachises. In almost all species where the secondary rachises are channelled or flattened on the abaxial surface they have a terete portion at their extreme base which forms a discontinuity between the primary and the secondary rachis. This is absent in the terminal pinna whose abaxial channel is continuous with that found in many species in the upper part of the primary rachis.

In the New World there is one species which does not fit into this morphological series, viz. *L. stenomeris* (fig. 46). It has dimidiate, yet deeply incised pinnules with uninerval sori but is bipinnate *cum impari*. This type of leaf is much more common in the Indo-Malayan region; examples are *L. blumeana* (Hook.) Kuhn, *L. schlechteri* Brause, *L. tenuifolia* Bl. and *L. versteegii* (Christ) v.A.v.R.; some of them are even simply pinnate (*L. schlechteri* and sometimes *L. versteegii*). Possibly the fine dissection, leading to capillary divisions in some Malaysian species, is a secondary phenomenon; but it is not impossible that it was retained as a primitive character that did not evolve further than the dimidiate stage of the pinnules whereas the architecture of the divisions of higher order advanced (that is, became simpler) independently.

When the marginal incisions become very shallow to obsolete, the conditions for the development of one uninterrupted sorus per pinnule are developed. This type of pinnule, entire or almost entire, and with a continuous sorus, is found in the majority of the American species. The sorus is found along the upper and outer margin, as it is situated on the commissure between the vein-ends, and in a dimidiate pinnule the veins radiate from the lower margin and end along the upper and outer edge. This type, with continuous sori, is less common among the Asiatic species, but a few of them represent striking parallels to American representatives, such as *L. scandens* resembling *L. lancea* with which it was confused for a long time (see p. 252), *L. borneensis* approaching *L. guianensis* ssp. *guianensis*, etc. Intermediates between continuous and interrupted sori are not common. In the New World examples are found in *L. ovoidea* (fig. 39) and *L. botrychioides* (fig. 47, 48), which in most pinnules have continuous sori but where in large pinnules often two incisions occur that interrupt the sorus, one in the upper and one in the outer margin.

Something quite different are the so-called incompletely fertile pinnules. In many species of *Lindsaea* quite sterile leaves are rare on full-grown rhizomes. One of the few exceptions is L. *guianensis*; besides, *L. cubensis* has somewhat dimorphous leaves (sterile versus fertile); in *L. stricta* the basal part of otherwise fertile leaves is mostly sterile. But this is rather exceptional, and in some species the author has not seen a single wholly sterile leaf, a condition which is just the opposite of what is observed in some other genera, for instance *Elaphoglossum*, where the scarcity of fertile leaves often drives the Pteridologist to despair. The sterile leaves of *Lindsaea*, where they occur, tend to have crenate, sometimes more deeply incised pinnules, whereas fertile ones of the same species may be quite entire. This is particularly true for sterile leaves found on juvenile rhizomes, e.g. in the Old World species *L. macraeana* (see Holttum, 1954, fig. 185, and Christ, 1910, fig. 46 and 47). The phenomenon has been interpreted in a phylogenetic sense; juvenile plants were believed to produce leaves of an ancestral type. This kind of explanation, strongly reminiscent of Haeckel's biogenetic base-law, although it has proved to be useful in some cases (for instance the derivation of the pseudopedate leaf-pattern of *Adiantum pedatum* from a bipinnate one, see Wagner, 1952 a), should be applied with great caution. Sometimes leaves are found that are intermediate between the sterile and fertile condition; sori occur in a part of the lamina only and tend to be interrupted, not rarely uninerval, in species with normally continuous sori. These short sori are most often found at the border of zones with normal fertility; sometimes, for instance, the inner part of a pinnule may bear sori occupying several veins while the outer sori are uninerval. The margin of such incompletely fertile pinnules or portions of pinnules is often crenate in the same way as in sterile pinnules of the same species. These incompletely fertile leaves or pinnules are not of very frequent occurrence but are very confusing as they diverge from the normal pattern of the species; they cannot be keyed out with the key presented in this paper where great value is attached to the structure of the sorus in the normally fertile condition.

It seems likely that the explanation of this phenomenon has to be sought in connection with phytohormones. It does not seem a very daring guess to assume that the production of fertile leaves in ferns is regulated by phytohormones comparable to the flowering hormones demonstrated in many Angiosperms. The incompletely fertile parts may then be supposed to have developed with a supply of this hormone insufficient to induce the formation of complete, normal sori.

In this context a few species must be mentioned that have interrupted, largely uninerval sori but only shallow marginal incisions which cannot be held responsible for the lack of a commissure between the fertile vein-ends. These species have been separated as a genus (or subgenus), *Odontoloma* J. Smith, but certainly not all of them are closely related within the genus *Lindsaea*. But for the constant occurrence of very short sori one would be inclined to take the leaves of these species for incompletely fertile ones. In the New World there is only one representative of this type, *L. parkeri* (fig. 40); the Old World has several of them, the most widespread being *L. macraeana*. We must thus express the relation between not or little incised pinnules and continuous sori in a more cautious way; we can state only that an uninterrupted margin provides the opportunity for the development of a continuous sorus, but that the latter is not a necessary consequence of the former.

A further simplification, rare among species with incised pinnules, but common among forms with entire pinnules and continuous sori, is the occurrence of simply pinnate leaves. In some species the leaves are exclusively or almost exclusively once-pinnate (*L. botrychioides*, *L. dubia*, *L. hemiglossa*, *L. schomburgkii*, *L. semilunata*, *L. ulei*), in many others once pinnate and bipinnate (occasionally even subtripinnate or tripinnate) leaves are regularly found side by side (e.g. *L. arcuata*, *L. lancea*, *L. parkeri*, *L. portoricensis*, *L. stricta*). This shows that the character: pinnate versus bipinnate is generally unreliable for diagnostic purposes, and it has consequently been used very little in the key to the species. This has not always been realized, and bipinnate or subtripinnate specimens of ordinarily less compound species have sometimes been described as new varieties. Moreover, juvenile specimens bear less compound leaves than adult ones; therefore, on rhizomes which are in a transitional stage, simply pinnate leaves may be found together with bipinnate ones, the latter representing the normal pattern. The former are then, however, mostly sterile. Incidentally, this shows that Haeckel's law is not applicable here; simply pinnate leaves appear in the development of a single plant before the bipinnate ones, but in a phylogenetic sense they are very probably more derived.

In all species where once- and twice-pinnate leaves occur side by side the structure of the ultimate divisions is exactly the same. For this reason they are in this paper consistently called pinnules, whether they occur on pinnate, bipinnate, or subtripinnate leaves; it would not have been logical to speak of pinnae in the first, of pinnules or secondary or tertiary pinnae in the second case, as they are all alike in structure and undoubtedly homologous. The term segments has been reserved for divisions that are not completely free, or has occasionally been used in a general sense, including both pinnules and segments in the more restricted meaning.

Another character that shows certain variations where a primitive and a derived pattern can be detected is the structure of the pinna- or (in simply pinnate species) lamina-apex. In all species with incised pinnules and in many with entire ones the upper pinnules gradually decrease in size towards the apex of the pinna or lamina and are finally and often very gradually confluent into a terminal segment (see, e.g., fig. 27, 51, 65). In other forms, such as L. *quadrangularis* ssp. *terminalis* (fig. 49) and *L. surinamensis* (fig. 58), the reduction in size of the upper pinnules is considerably less evident, and one or two only are joined by a wing to the terminal segment which is thus almost free; in these species it has a peculiar shape, ± triangular, asymmetric at the base, with two unequal lobes, the largest and lowest found on the side opposite the uppermost lateral pinnule, but otherwise entire, or sinuate in the lower part. Apart from the two basal lobes the origin of this segment from confluent reduced pinnules is hardly evident. The next step is taken when the terminal segment becomes quite free and may be called a terminal pinnule. It is interesting to note the presence of a correlation between this process of simplification of the architecture of the apex and the overall dissection-pattern of the leaf; all species with a free terminal segment, namely, *L. lancea*, *L. latifrons*, *L. hemiglossa*, *L. semilunata*, *L. schomburgkii*, and *L. ulei*, have simply pinnate leaves, and in all but the two first-named species this is always the case. Here also the upper pinnules decrease often very little in size, and the number of lateral pinnules as a whole is rather small.

In *Lindsaea lancea* the terminal pinnule is of the asymmetric triangular shape described above (fig. 5–7, 79), but in the other species it is rather different. The apex becomes obsolete or is altogether wanting, i.e. the distal margin becomes flattened, the lateral lobes protrude strongly, the pinnule is approximately obtriangular, often transversal and approximately symmetric (see fig. 82). A central main vein (present in L. *lancea*) is apparently absent, but a trace of it can still be found. The keel formed by the junction of the margins bordering the abaxial groove of the rachis shortly enters the terminal pinnule; it lies to one side of the base, the side where the uppermost lateral pinnule is found. This can be explained by the assumption that one-half of the terminal pinnule is apparently formed by the largest, lowest lobe of the terminal segment, whereas the other half consists of the other lobe and the almost obsolete apex. The fact that the distal margin is usually slightly bulging at this side of the terminal pinnule shows that a trace of the apex is still present. The keel, which in *L. lancea* evanesces in the midvein, is thus an indication where the apical shank that contains it should be looked for. Fig. 78, showing the upper part of the lamina of *L. ulei*, gives an illustration of what has been described above. Even if there is no bulging portion of the distal edge, as is sometimes the case, the asymmetry in venation at the base of the terminal pinnule is still there.

These Lindsaeas with large terminal and few lateral pinnules are probably to be regarded as the source whence the simple-leaved species have sprung that are so outstanding among the American representatives and, as a matter of fact, unique in the whole genus. Particularly *L. ulei* agrees with them in such characters as rhizome-scales, dark and (at least in the lower half) terete petioles and strongly intramarginal indusia; furthermore they are approximately sympatric. It seems likely that the species of this group, the section *Haplolindsaea*, originated from a form allied to *L. ulei*, or perhaps from this species itself, through suppression of the lateral pinnules and basipetal expansion of the lateral lobes of the terminal pinnule, resulting in an approximately round lamina. It may be significant that the leaves of juvenile plants of *L. cyclophylla* are bean-shaped or semi-elliptic with very little lateral basipetal expansion (fig. 90), but again, the value of such characters observed in juvenile plants is questionable. The acute basal lobes of the lamina sometimes found in *L. sagittata* (fig. 88) may be a remnant of the lateral horns of the terminal pinnule present in *L. ulei* and some allied species. WAGNER (1952 b, 1954 b) believed the species with a midrib to be the basal type (he called it *L. sagittata*, but his figure (1952 b, fig. 9 I) represents *L. reniformis*, where he apparently mistook the median prolongation of the sclerotic patch at the base of the lamina for a midrib), and the midrib-less species *)

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*) There may be a short midrib in the sclerotic patch at the base of the lamina which would be only visible in sections.

derived from it through loss of the main vein; but the species grouped around *L. ulei* have no midrib to speak of in their terminal pinnules, whereas that of *L. sagittata* is quite pronounced and long. It seems more likely that the prolongation of an originally obtuse apex, as found in *L. cyclophylla* (fig. 90, 91) and *L. reniformis* (fig. 89), to the long acumen of *L. sagittata* is a secondary phenomenon, which was accompanied by a stronger development of the vein catering to this apex, i.e. to a larger portion of the lamina than the other veins. Then *L. reniformis* or *L. cyclophylla* would represent the basal type of the section. An alternative solution that cannot be completely dismissed is that the simple-leaved species did not arise from a form resembling *L. ulei* but from a hypothetical form with an acute terminal pinnule provided with a median main vein not unlike simply pinnate forms of *L. lancea*.

A structure peculiar to the section *Haplolindsaea* is a patch of black sclerotic tissue on the abaxial side of the lamina above the insertion of the petiole. Its apex is prolonged into a tapering extension overlying the base of a vein in *L. reniformis, L. sagittata*, occasionally also in *L. cyclophylla*. The function of this structure is probably mechanical, but no details are known.

From this discussion follows the unnaturalness of DIELS' inclusion of *L. reniformis* and *L. sagittata* in *Schizoloma* (1902). With *L. ensifolia, L. walkerae, Isoloma*, or *Schizolepton* which constitute the rest of Diels' genus they have little in common, except the lack of dimidiate pinnules. If Diels had been consistent, he would have been obliged in such a species as *L. schomburgkii* to put the terminal pinnule in *Schizoloma* and the lateral ones in *Lindsaea*!

Finally, a few species have to be dealt with that do not fall within the sequence of forms outlined above and are not or only in a vague way connected with the bulk of the American species, or that are outstanding by very peculiar characters.

Firstly *L. meifolia* and *L. pendula*, which together form the section *Crematomeris*. These species (fig. 41–43) are very remarkable by their pendulous pinnules or—in *L. meifolia* in places where the leaves are more than twice pinnate—secondary pinnae. In order to attain this position twisting occurs, strangely enough, in two places. The secondary rachises which depart from the primary rachis at approximately right angles—hardly ever found in other sections—are twisted over 90° at their bases in such a way that the morphologically adaxial side with the groove faces the apex of the leaf, the terete abaxial side the base. The organs inserted on the secondary rachises, pinnules or tertiary rachises, are again bent over 90° at their bases, all to the basiscopic side, which makes them pendulous. To a certain degree this is also observed in the pinnules (of third order) in the basal part of the pinnae in *L. meifolia;* the pinnules in the apical part of the pinnae are thus in the same plane as the secondary rachises in the basal part, as both are of the same (second) order, and the pinnules on the tertiary and in the apical part of the secondary rachises are in planes that are at right angles to each other, although both are pendulous. This is not always clearly observed in herbarium specimens, as all organs are pressed in the plane of the sheet. In *L. pendula* the terminal pinna joins the lateral ones in being bent over to one side and bearing also pendulous pinnules (fig. 42).

It is very tempting to assume that the pendulous position of the pinnules on an erect rachis arose as an adaptation to the open habitats in which *L. pendula* occurs (savannas and bogs), and it is probably of biological importance in this species; *L. stricta*, another species occurring mostly in open habitats, is also reported by collectors to have stiffly erect leaves with almost vertical pinnules. Yet *L. meifolia* has invariably been collected in moist dense forests! The phenomenon originated apparently without connection with a special milieu, but, once it was present, enabled *L. pendula* to colonize an open habitat, or was at least advantageous in the process. Incidentally, the step from incised to entire pinnules linked with that from decompound to bipinnate *cum impari* leaves can be beautifully observed in these two closely related species.

Among the American species there is only one with anastomosing veins and equal-sided pinnae, namely, *L. macrophylla* (fig. 92). The reason for the inclusion of this species in the genus, although tentatively in a separate subgenus, has already been discussed. It may be of interest to note that the occurrence of anastomosing veins in the genus *Lindsaea* is not limited to species with comparatively large, undivided segments. The Asiatic species with anastomosing veins often placed in the subgenus (originally genus) *Synaphlebium* J. Smith have dimidiate pinnules, and in some of them the pinnules are so narrow that only a few anastomoses per pinnule are left, e.g. in *L. sinuato-crenata* v.A.v.R. On the other hand, species with large undivided laminal parts such as *L. taeniata* and the simple-leaved forms have quite free veins. The relation between the degree of dissection and anastomosis: the less dissected, the more anastomoses, reported, for instance, in *Tectaria* (COPELAND, 1947, p. 129), and in *Cnemidaria* versus *Cyathea* (id., l.c., p. 98) is not met with in *Lindsaea*.

Almost all neotropical species have laminae that are truncate at the base, i.e. the basal pinnae or pinnules are not or hardly shortened. The only exception is formed by the section *Tropidolindsaea* which occupies a rather isolated position. In the three species forming this section, *L. seemannii*, *L. pratensis*, and *L. protensa*, the lower pinnules are very gradually reduced and farther apart (fig. 32). More about this group is found on p. 136; it is sufficient to point out in this place that *L. seemannii*, with incised pinnules, seems to be the most primitive member of the section, whereas *L. pratensis* with almost always continuous and particularly *L. protensa* with wholly continuous sori and small, very numerous pinnules are apparently more derived.

A peculiar development of an almost equal-sided pinnule from a dimidiate one is observed in *Lindsaea herminieri* and especially in *L. taeniata*. In the first species the apex of many pinnules is protracted into a long, obliqualy ascending point with an approximately median (diagonal) main vein; the sori are borne on both of its sides, as one side is formed by the upper, the other by the outer margin (fig. 60). A similar phenomenon is observed in a caudate form of *L. arcuata.* In *L. taeniata* this is developed in such a way that the protracted apex forms the greater part of the pinnule; the dimidiate portion is quite short, the (morphologically) outer margin is almost a prolongation of the lower margin, which therefore seems to be soriferous in its outer part (fig. 62). Technically *L. taeniata* would answer the diagnosis of the genus *Schizoloma* of most authors, although its closest relative is undoubtedly *L. arcuata*, which has little in common with *L. ensifolia*, the type species of *Schizoloma.*

When the forms of the New World in general are compared with those of the Old World, it springs to the eye that whereas the primitive forms of both regions are comparable and often similar, the derived ones are different. The highly condensed forms with few large lateral and a large free terminal pinnule or even with simple lamina are almost absent in the Old World, the only representative of that type known to the other being a form of *L. scandens* which duplicates *L. lancea.* On the other hand, species with dimidiate but incised, usually rather small pinnules abound in the Indo-Malayan region but are very scarce in the Western Hemisphere (*L. virescens*, *L. stenomeris*). The same is true for species with entire of almost entire pinnules but interrupted sori (some species of the section *Temnolindsaea* in America).

9. LINDSAEA AND ADIANTUM

As has been pointed out above, the first species of *Lindsaea* were described under *Adiantum*, and still the two genera are not rarely confused by collectors and in preliminary sorting in herbaria. The superficial resemblance of leaf architecture and pinnule structure between the two genera is indeed striking, and so many types in one of them are matched by species in the other that we may speak of parallel development.

In the neotropical Lindsaeas this is even more noticeable than in the paleotropical ones, although, of course, the corresponding types of *Adiantum* do not necessarily occur in the same hemisphere. The common dimidiate type of *Lindsaea* represented by such species as *L. lancea* and *L. quadrangularis* has its counterpart in the forms usually united under *Adiantum tetraphyllum* which is almost equally widespread in the Western Hemisphere. The transition to simply pinnate forms, found in several species of *Lindsaea* (see p. 49/50), is met with in such species as *Adiantum obliquum.* The simple-leaved type, so outstanding among the American Lindsaeas, is duplicated in the well-known *Adiantum reniforme*, but this fern, occurring chiefly in Macaronesia, is a xerophyte, as opposed to the species of *Lindsaea* section *Haplolindsaea*, which, though not infrequently growing on rocks, avoid truly dry or seasonally dry habitats. The species of *Adiantum* with approximately equal-sided, mostly tongue-shaped pinnae or pinnules, with a tendency towards anastomosis of veins, such as *A. dolosum* and *A. adiantoides*, can be compared to the Lindsaeas with similar ultimate divisions that are usually included in *Schizoloma*, *L. macro-*

phylla and *L. ensifolia*, also with reticulate venation; as a matter of fact, the author found several specimens of *Adiantum dolosum* determined as *Lindsaea macrophylla*. But this type of leaf is more common in *Adiantum* than in *Lindsaea*. *L. stricta*, the species from open habitats with small, rigid erect pinnules resembles to a certain extent *Adiantum serratodentatum* that grows in similar situations. In the forests of eastern Perú the miniature *Lindsaea spruceana* has been found, and in the same region occurs its counterpart *Adiantum humile;* and so on. It is not so easy to find an obvious counterpart to the highly compound species, e.g. *L. bifida;* but it seems reasonable to compare them to the numerous species of *Adiantum* with decompound or bi—tripinnate leaves and cuneate pinnules (*A. raddianum*, *A. tenerum*, etc.). The author believes these species of *Adiantum* to represent the most primitive type of that genus, the dimidiate and equal-sided forms being more derived, probably along several lines of descent. This derivation did not necessarily and even not probably happen in the same way as in *Lindsaea*, through reduction of segments and their fusion, but the dimidiate and the equal-sided Adiantums are certainly a simplified type as compared with the cuneate ones, as they are (at least the neotropical ones, with which the author is acquainted to a certain extent) bipinnate *cum impari* or simply pinnate, whereas many cuneate ones are decompound. There are, of course, other ways in which the cuneate type specialized and produced simplified types, leading, for instance, to a once-pinnate leaf with cuneate leaflets (*A. deflectens*), a pseudopedate pattern (*A. pedatum*); etc. In this connection it is probably significant that we have a third genus with highly divided and with dimidiate (as well as many other) types of leaves, namely, *Asplenium*. It seems likely that here, too, at least some of the highly divided forms (in the New World for instance those grouped with *A. rutaceum*) represent the more primitive leaf-type, and HOLTTUM (1947) regards them as such. This seems to be corroborated by the fact that in the genus or subgenus *Loxoscaphe* highly dissected leaves are found of a type comparable to, for instance, that of *Lindsaea bifida*; and Holttum believed *Loxoscaphe* to link the Asplenioids with the Davallioids. It should be mentioned, however, that WAGNER (1952 b, p. 140/141) presented anatomical and morphological and MANTON & SLEDGE (1954) cytological evidence against this supposed relationship of *Loxoscaphe* with the Davallioids.

There are, of course, points of difference and cases of peculiar, unmatched types in *Lindsaea* versus *Adiantum*. The highly dissected, yet dimidiate types in *Lindsaea* (*L. stenomeris*, *L. blumeana*, etc.) have nothing really comparable in *Adiantum*, and the pseudopedate leaf of *Adiantum pedatum* and others has not been developed in *Lindsaea*. But as a whole there are few fern genera showing such a striking parallel development as *Lindsaea* and *Adiantum*.

The genus *Didymochlaena*, the only other instance of a fern genus with dimidiate pinnules known to the author, occupies a rather isolated position among the Dryopteridoid ferns; its derivation is unknown. DICKASON (1946) associated it with the Lindsaeoids, apparently on account of the shape of the pinnules alone, a most unnatural procedure, as all other characters point to Dryopteridoid affinity. Even fragments can be easily distinguished by the scaly rachises and the teeth at the bases of the pinnules.

10. Subdivision of the genus

After the account of the morphology and the supposed evolutional tendencies of the genus *Lindsaea*, it will be described in the following how these data have been used formerly and are being used in the present study to subdivide the genus into as natural as possible taxa of lower rank, above the rank of species.

The various ways in which older authors have arranged the species in groups according to more or less—mostly less—natural characters need not concern us here, as far as no names were attached to these groups.

Hooker (1844–46) distinguished two subgenera: *Eulindsaea*, with "simple or forked", i.e. free, veins, and *Schizoloma* (published as a genus by Gaudichaud), with more or less anastomosing veins.

Moore (1857) based his subdivisions on the shape of the segments; these were isomerous, with a midrib, in his subgenus *Isoloma* (originally a genus of J. Smith), and flabellate or dimidiate, ecostate, in *Eulindsaea*.

Baker (1868) more or less combined these ideas and recognized four groups: *Eulindsaya*, with unilateral, free-veined pinnae (i.e., pinnules), *Isoloma*, with equilateral, free-veined divisions, *Synaphlebium* (a genus of J. Smith), with dimidiate segments and reticulate venation, and *Schizoloma*, with equilateral pinnae and anastomosing veins. These groups appear also in his treatment in Flora Brasiliensis (1870), except the third, which is not represented in the New World.

Keyserling (1873) had five subordinate groups, probably intended as subgenera: *Eulindsaya*, with dimidiate segments and mostly continuous sori, *Odontoloma* (originally a genus, created by J. Smith), with similar segments and interrupted sori, *Paralindsaya*, with cuneate segments and continuous sori, *Stenoloma*, also with cuneate segments but short, bi- to quadrinerval sori and spinose rachises, and *Isoloma*, similar to the previous group, but with unarmed rachises. The latter is a complete misinterpretation of J. Smith's genus of the same name on which it is based; Keyserling listed "*Davallia*" (= *Sphenomeris*) *retusa* as an example. *Paralindsaya*, the only group published as new, is based on incorrect morphological interpretation, as the segments of its only species, *L. linearis*, are no less dimidiate than they are in "*Eulindsaya*", though this is less evident because of their reduced length.

Diels (1902), who excluded *Isoloma* and *Schizoloma* from *Lindsaea* and put the highly compound species in *Odontosoria*, consequently restricting *Lindsaea* to the dimidiate types, had two sections, *Eulindsaya*, with free veins, and *Synaphlebium*, with reticulate veins. In the first section two subordinate groups appear, presumably intended as series: *Pinnatae*, with simply pinnate leaves, and *Bipinnatae*, with at least partly bipinnate leaves. It has been shown already that this criterium is next to useless; moreover these groups were not typified and can be ignored.

CHRISTENSEN (1906, p. xxx) recognized four subgenera, namely, *Eulindsaya*, based on *L. lancea*, *Hymenotomia* (based on a genus published by Gaudichaud), with *L. microphylla*, *Odontoloma*, typified by *L. repens*, and *Synaphlebium*, with *L. decomposita*. The first subgenus was divided in two sections, *Paralindsaya* Keyserling (see above), and *Lindsaynium*, based on Fée's genus, erected for *L. rigida*. It is not clear in which of these sections Christensen wanted to put *L. lancea*, the type of the subgenus; at any rate, *Lindsaynium* does not deserve recognition. Fée was impressed by the "marginal vein", for which he mistook the thick sclerotic marginal strand of *L. rigida*.

Later authors did not contribute anything new; nothing original appears, for instance, in VAN ALDERWERELT VAN ROSENBURGH'S treatment (1908).

The writer has pointed out already (p. 102/103) that he prefers to maintain *Schizoloma*, typified by *Lindsaea ensifolia* Sw., as a subgenus, although with misgivings. As far as the American species are concerned, all but *Lindsaea macrophylla* go then in the other subgenus "*Eulindsaea*", which according to our present rules of nomenclature should bear the name *Lindsaea* unaltered (Art. 22). In this subgenus the following sections are recognized (Latin diagnoses for those which are new are provided in the taxonomic part):

I. *Pseudosphenomeris*

Leaves decompound; ultimate segments not pendulous, cuneate, or rarely dimidiate, incised pinnules. This is the most primitive group; it includes the neotropical *L. bifida*, *L. sphenomeridopsis*, and *L. virescens*. Close relatives, especially of the two first-named species, in the Eastern Hemisphere are *Lindsaea millefolium* Kramer, nom nov. [*Davallia decomposita* Baker, Jo. Bot. 22:141 (1884); *Odontosoria decomposita* (Bak.) C. Chr., Ind. Fil. 465 (1906); *Sphenomeris decomposita* (Bak.) C. Chr., Dansk Bot. Ark. 7:78 (1932); *Stenoloma decompositum* (Bak.) C. Chr., Ind. Fil. Suppl. 3:173 (1934); not *Lindsaea decomposita* Willd., 1810], from Madagascar, and *Lindsaea eberhardtii* (Christ) Kramer, comb. nov. [*Odontosoria eberhardtii* Christ, Journ. de Bot. 21:235 (1908), *Stenoloma eberhardtii* (Christ) Ching, Sinensia 3:338 (1933)] from Annam and Hai-nan. Perhaps eventually also *L. microphylla* from Australia, New Zealand, and New Caledonia will have to be included in the same section.

II. *Crematomeris*

Leaves decompound or bipinnate *cum impari*; secondary rachises patent under an angle of ca. 90°, twisted at their bases, the channelled adaxial side acroscopic, the terete abaxial side basiscopic; segments of the second order pendulous, divided or entire. This section is, through *L. meifolia*, related to the preceding group, but not very closely. The morphological details are discussed on p. 130/131.

III. *Temnolindsaea*

Leaves bipinnate *cum impari*, rarely simply pinnate. Pinnules dimidiate, not pendulous, shallowly or occasionally more deeply incised; sori interrupted, occupying one or mostly a few veins. Here belong the species grouped with *L. klotzschiana; L. parkeri* is doubtfully related. The latter species has been placed in *Odontoloma*, but that genus, reduced to subgeneric rank by Keyserling but perhaps better to be made a section, is quite different in its long-creeping or rather scandent rhizomes, at least if typified by *Dicksonia repens* Bory, not by *Lindsaea tenuifolia* Blume, as was done by Copeland.

IV. *Lindsaea*

This section is discussed at the end.

V. *Haplolindsaea*

This includes the forms with simple lamina and is probably derived from the preceding section; see p. 129.

VI. *Paralindsaea* (Keyserling) C. Chr.

Leaves simply pinnate, or the fertile ones bipinnate, with dimidiate pinnules decreasing in size towards the apex; leaves dimorphous, the sterile ones short, ± spreading, the fertile ones longer, erect. The type species of this section is *L. linearis* from Australia, etc., as indicated by Keyserling. *L. cubensis*, the American species grouped with it in the present study, resembles it in dimorphism and in the shape of the pinnules, but differs by sometimes bipinnate fertile leaves and monolete spores. The alliance of the two species is not entirely certain, and *L. cubensis* is only tentatively placed in the present section; it is, however, isolated among the other American species.

Another species to be placed in this section, but without doubt, is *L. dimorpha* Bailey (*L. heterophylla* Prentice, non Dryander) from north-eastern Australia; it differs from *L. linearis* chiefly in its incised sterile (sometimes also fertile) pinnules. It is probably connected with *L. microphylla* through *L. incisa* Prentice, both last-named species from the same region, which are, however, not dimorphous and should probably be placed in another section.

VII. *Tropidolindsaea*

This is the group of *L. seemannii*, confined to the Caribbean region and the northern Andes. The leaves are simply pinnate, gradually reduced above and below; the rachis is keeled (*L. seemannii, L. pratensis*) or narrowly rounded (*L. protensa*) on the abaxial side. The scales are very large and broadly lanceolate or ovate, clathrate in *L. seemannii;* the spores are monolete. The sporangia are of a type slightly different from the other species, as the indurated part of the annulus does not quite reach the stalk. The group of species is quite isolated among the American species, probably even in the whole genus. The only species to which alliance is evident is *L. viridis* Colenso from New Zealand. It has bipinnate or mostly bipinnate + pinnatifid leaves;

otherwise it agrees rather closely with the American group, especially with *L. seemannii*, whose incised pinnules on simply pinnate leaves may be regarded as simplified derivatives of the pattern of *L. viridis*. Characters of agreeance are the abaxially keeled petiole and rachis, upwards and downwards reduced lamina (in *L. viridis* not strongly reduced below), the sudden transition from the dark primary rachis to the pale secondary rachis or base of the pinnules, the sporangia, and the monolete spores. The scales of *L. viridis* are narrowly lanceolate, of a type otherwise found in *Sphenomeris*, but in their apical part they are distinctly clathrate, as in *L. seemannii*. The inclusion of *L. viridis* in *Lindsaea* is perhaps not justified; it may represent a specialized offshoot from *Sphenomeris* that gave independently rise to dimidiate species, or it may be close to the common source of *Lindsaea* and *Sphenomeris*. Perhaps the section *Tropidolindsaea* would better be made a subgenus or even excluded from the genus; but again, this should be decided after thorough study of all species in the Eastern Hemisphere.

Finally the section *Lindsaea* is to be discussed more at length. It includes the bulk of the neotropical species, but probably none from the Old World. The type species of the genus must be included; there has been some controversy as to which species should be selected as type.

John Smith (1875, p. 267) selected as type *L. trapeziformis*, in which selection he was followed by Christensen (1906, p. xxx) and Ching (1940, p. 217). Copeland (1929, p. 83), on the other hand, argued that this was incorrect, as *L. trapeziformis* was not among the three species listed by J. E. Smith in his original publication of the genus (1793, p. 413: "Exempl. Gener.: Adiantum guianense Aubl., sagittatum ejusd., stricta Swartz"). He chose (1947, p. 53) *L. guianensis* as type. His argumentation is, however, not conclusive. Plate IX accompanying J. E. Smith's paper shows (fig. 4) a pinnule on a rachis-fragment and a detail of the sorus, said to belong in the "Explicatio Tabulae" to "Lindsaea, forte nova species". Dryander himself stated that this illustration represented his *L. trapeziformis* (apparently a reduced axillary pinnule; the shape is not at all like typical *L. trapeziformis* = *lancea*, nor like Dryander's figure of that species on his pl. 9). *L. trapeziformis* was therefore included in the original material on which the genus was based; moreover, the species cited by J. E. Smith were merely examples and apparently did not claim to constitute the whole genus, and no transfer was made, which was left to Dryander in his paper four years later. Therefore the present author cannot see any objection against the maintenance of *L. trapeziformis* as type-species of the genus.

It is very difficult to arrange the rather numerous species of the section *Lindsaea* in subsections or series. Certain groups of rather closely related species can be distinguished, but generally the morphological similarities are what one might call reticulate, which makes it very difficult to establish clear-cut groups of closer affinity.

Two groups can, however, be segregated from the majority of species. Firstly, *L. ovoidea* and *L. botrychioides*, distinguished by slightly interrupted sori in the largest pinnules, forming together the sub-section *Subinterruptae*. Secondly, the species with a large terminal pinnule which is quite free from the upper lateral pinnules, brought together in the sub-section *Terminales*: *L. ulei*, *L. hemiglossa*, *L. latifrons*, *L. lancea*, *L. semilunata*, and *L. schomburgkii*. It is not quite certain whether all these species represent one phyletic line, and the distinction from the third sub-section *Decrescentes*, comprising all other species of the section, with reduced upper pinnules ± confluent into a terminal segment, is not very sharp, as some forms, e.g. *L. surinamensis* and *L. quadrangularis* ssp. *terminalis*, often have an almost free terminal segment. This element of doubt seems to be adequately expressed by the assignation of subsectional rank to the group.

The section *Lindsaea* and the sub-section *Decrescentes* as well as a few others are not easy to define in such a way that all Old World species are excluded; the author has to leave this to a monographer of those forms, who, after all, may find some species that have to be put side by side with neotropical ones.

11. APPLICATION OF CATEGORIES BELOW THE RANK OF SPECIES

It may be necessary to explain briefly the entities and the rank assigned to them that are recognized in this paper. No comment on the species- concept seems to be required, but below the rank of species three categories have been employed about which some elucidation may not be out of place. These categories are the subspecies, the variety, and the forma, and their use side by side is to a certain extent in disagreement with the custom of many contemporary taxonomists who often have a favorite rank (most commonly the variety) to which all infraspecific taxa are assigned, while others, known as splitters, have a tendency to raise each entity they recognize to full species rank.

In the present revision all those forms that are sufficiently clear-cut but are very close together, i.e. closer than most or all other related species, and show at least some degree of geographic isolation, have been combined under one species as *subspecies*. The author fully realizes that it is more or less a matter of taste whether they are treated as subspecies or species, and he would not strongly object to assign species rank to *L. guianensis* ssp. *lanceastrum* or the subspecies of *L. quadrangularis* described below as new.

As *varieties* those forms are recognized that differ from each other in one or a few characters of rather little relevancy, where intermediates are found, though not very often, and where no geographic isolation is observed. In some cases, e.g. in *L. stricta* var. *parvula* or *L. lancea* var. *remota*, there are indications that some of these forms represent ecotypes, restricted to or preferring peculiar habitats; the fact that these forms occur within the area of the entities to which they are most closely related (though not throughout their area), and that intermediates, compared to the total number of known specimens, are not very rare, seems to justify their treatment as varieties.

Forms that are aberrant in one rather trivial character only, but by virtue of this are outstanding among the bulk of the specimens, or that differ by a combination of a few characters, but show rather numerous intermediates, either by combination of characters, or by intermediate stages, are distinguished as *formae*. If the series of intermediates becomes so large that the localization of the boundary between typical form and intermediate on the one hand, and intermediate and special form on the other hand, becomes quite arbitrary, the aberrant specimens are included in the species without any special name (examples are the simply pinnate, dark-petioled form of *L. lancea* and the thin, lax form of *L. stricta*). It is possible that in these cases cytological investigation will show two (or more) extremes, with a long series of intermediates formed by introgression; but such an assumption can hardly be made on the base of morphological data taken from herbarium-specimens only

The different types of diversity of intraspecific units are, of course, not sharply distinct, and future investigations, particularly study in the field, may show that certain forms have been put here in the wrong category. But with the data available at the present time, and the directions for application of infraspecific ranks described above, the author has been able to assign most forms to a certain rank without too much hesitation.*)

Hybrids. Great caution has been observed in calling intermediate forms hybrids. In a few cases there are strong indications that certain forms (notably *L. dissecta* and a few doubtful ones discussed at the end) are of hybrid origin, because characters of two species and abortive sporangia or spores are combined in them. In other cases of intermediate specimens, where nothing abnormal about the spores could be observed, the assumption of hybrid nature could not be made with reasonable certainty, particularly because in the genus *Lindsaea* where few species possess absolutely dependable differentiating characters or combinations of characters aberrant specimens are found in many species. Here, again, we cannot but hope that, a.o., cytology will help to clear up such problems; as a matter of fact, cytological research has already brought to light the presence of hybrids even among species or species-groups where they had not been expected (MANTON, 1950; MANTON & SLEDGE, 1954).

12. GEOGRAPHICAL DISTRIBUTION

Lindsaea is mainly a tropical genus; the bulk of the species occur between the tropics, especially in the Western Hemisphere and in south-east Asia. Whereas a number of species occur in Madagascar (seven are listed by CHRISTENSEN, 1932, but several referred to *Schizoloma* and *Sphenomeris* have to be included, which brings the total number to about fifteen) and the adjacent islands, continental Africa is remarkably poor in having only the widespread *L. ensifolia* (*Schizoloma ensifolium*), reported from Natal and West Tropical Africa.

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*) Here Kunze may be quoted who complained (Linnaea 21:229, 1848): "Antequam Lindsayae . . . locis suis a pteridologo quodam perito studiose observantur, quid sit species, quid varietas aegre dijudicatur."

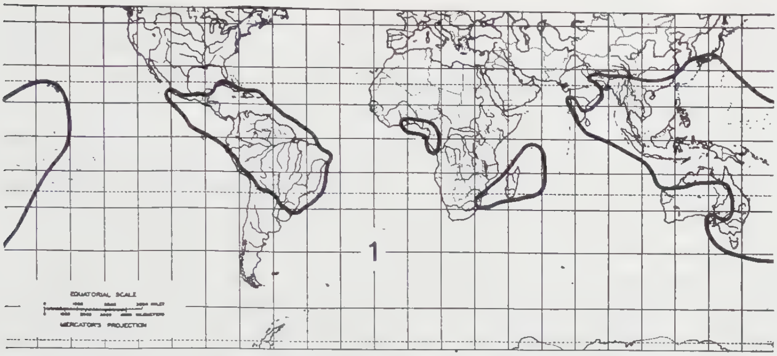
The area of the genus as a whole extends, however, considerably beyond the tropics in certain regions, especially in Japan (ten species, three reaching Honshu, see TAGAWA, 1937), Australia (two species in Victoria, see EWART, 1930, and one in South Australia, according to BLACK, 1922), and New Zealand (three species listed by DOBBIE & CROOKES, 1952). In the Pacific the genus reaches the Marquesas with two (BROWN & BROWN, 1931) and Hawaii with one species (CHRISTENSEN, 1925).

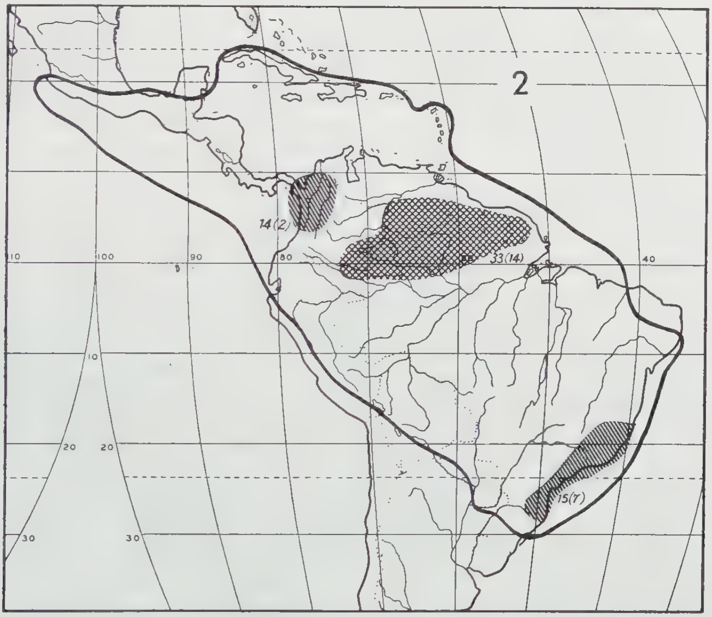
In the New World the genus is distributed from south-western Mexico and Cuba in the north to Bolivia, Paraguay, and Rio Grande do Sul (Brazil) in the south. The reported occurrence of one species in Misiones, north-eastern Argentina, could not be checked by the author (see under *L. lancea*).

Map 1 gives an outline of the area of the whole genus; the limits of the distribution in the Old World shown there are only approximations, especially in China and Africa.

The species occurring in Mexico are mostly confined to the moist tropical South-East in the states of Chiapas, Oaxaca, and Vera Cruz, but one species mostly occurring in open habitats, *L. stricta*, extends to Jalisco (map 32). In the south the two species found in Rio Grande do Sul, *L. lancea* and *L. quadrangularis* ssp. *terminalis*, are forest-dwellers. No Lindsaeas have so far been collected in Florida and the Bahamas (where the allied genus *Sphenomeris* occurs), Yucatán, El Salvador (see STANDLEY & CALDERÓN, 1925, MAXON & STANDLEY, 1930, and LÖTSCHERT, 1954, none of which reports any Lindsaeas), the smallest of the Lesser Antilles (Saba, St. Kitts, Anguilla, etc.), the Galápagos Archipelago, the extreme north-east of Brazil (states of Rio Grande do Norte and Paraiba), the coastal areas of Perú and Bolivia, and the whole of Chile, including Juan Fernández (see map 2). The absence in most of these regions can be explained by their dry climate; but one would certainly except the presence of such species as *L. lancea* and *L. arcuata* in the remnants of forest on the volcanoes of El Salvador; also the complete absence from the moist temperate regions of central Chile is not easy to understand in the light of the presence of several species at approximately the same latitude in Australia and New Zealand. The climate of the latter regions is, however, warmer and/or moister than of central Chile (Cf in New Zealand, Cfa, Cfb or Csa in the temperate parts of Australia where the genus occurs, as opposed to Csb and Cfc in central Chile, in Köppen's classification of climates).

Only four of the species occurring in the New World can be called widespread, namely, *L. lancea*, (maps 37—41), *L. portoricensis* (map 25), *L. stricta* (maps 31—34) and *L. divaricata* (map 27). Most others are more or less restricted in their range, although it is often difficult to say how much, as too little collecting has been done in many regions to get an even approximately reliable picture of the distribution of such species. Species which can be said with some reasonable certainty to be narrow endemics are *L. herminieri* (Guadeloupe), *L. protensa* (Massif de la Hotte, Hispaniola), *L. pratensis* (Costa Rica) and *L.* cubensis (western Cuba and Isla de Pinos).





Map 1: Distribution of *Lindsaea* as a whole. Map 2: Distribution of *Lindsaea* in the New World. (Cross-hatched lines: primary centre of species-concentration; diagonal lines: secondary centres. See also p. 141/142).

The centre of species-concentration (see map 2) is the region of the Guiana-shield, sometimes called "Guayana" (a term used in the taxonomic part of this paper), extending from south-eastern Colombia to French Guiana and northern Brazil. Of 51 taxa in the rank of species, subspecies, or variety, which are sufficiently distinct to be used for phytogeographical analysis, 33 are present in Guayana; 14 of these are endemic, and 9 have their main distribution here. The Brazilian shield or Brasilia possesses 18 taxa, including 8 endemics; of the remaining 10, none occurs mainly but not exclusively in this region *). Brasilia, therefore, may be called a secondary centre. Another, but less pronounced, secondary centre is situated in the Andes, on the slopes of the approximately north-south-running valleys of the western Cordilleras of Colombia, and on the Pacific slope from El Valle (Valle del Cauca), Colombia, to Darien, Panamá. Here 14 forms are found, but only 2 of them are endemic, namely, *L. seemannii* and *L. taeniata*. Moreover, *Sphenomeris killipii* and *S. spathulata* are only known from this region. Of the 12 forms that are not restricted to this centre, 4 have their main distribution in Guayana, 6 occur there but also elsewhere, and only 2, *L. arcuata* (apart from two collections from Suriname referred to the caudate form of *L. arcuata*, but with misgivings) and *L. quadrangularis* ssp. *subalata*, are absent from that area. Almost all localities of these species in the Colombian sub-centre are situated to the west of the Eastern Cordillera, in what is called "Choco" by Schuchert **), i.e. the Pre-Mesozoic massifs of the Colombian borderland, largely composed of plutonic rocks. It seems likely that most of them reached this region from the Guianas before the main upheaval of the Andes *sensu stricto* in middle and late Tertiary times; thus they were more or less cut off from most other regions, but endemics were hardly developed. *L. seemannii*, endemic in the Choco region, is probably a relic species, belonging to a group of three rather closely allied species without obvious relatives in the Western Hemisphere, but with a more distantly allied species in New Zealand. The closest relative of *L. seemannii*, *L. pratensis*, probably reached the volcanoes of Costa Rica from the same massif or was developed as a local endemic. The third species of the group, *L. protensa*, occurs in a very restricted part of south-western Hispaniola, where it was collected on lateritic soil. It is probably of similar origin and its presence in Hispaniola is presumably connected with the fact that the Choco massif formerly extended into the Caribbean sea (SCHUCHERT, p. 638).

The poverty in taxa of the Andes and the West-Indian region is indeed remarkable. Outside the secondary centre in Colombia and adjacent Panamá there is no area that can be said to be rich in forms. Ecuador/Perú has two endemics on the eastern slopes which are very closely allied, and *L. spruceana*, once collected in eastern Perú, which is perhaps not a good species. Even Costa Rica which in other fern genera harbours a wealth of endemics has only one endemic *Lindsaea*, *L. pratensis*, dealt with before, and besides *Ormoloma standleyi*, extending to Chiriquí, Panamá. Otherwise only widespread species are found in the Andes; the only more restricted ones are *L. arcuata* and *L. klotzschiana*, the first occurring also in south-eastern Brazil and the second on the table-mountains of western Guayana. In the West Indies

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*) On map 2 only the south-eastern part of Brasilia is shown as a secondary centre, where the greatest concentration of species is found and which is floristically best known. The figures are slightly lower for this part of Brasilia than for the whole shield.

**) The geological data used in this paragraph were taken from GERTH (1941), SCHUCHERT (1935), WEEKS (1948), and BEARD (1949).

(exclusive of Trinidad and Tobago) there are but four endemics: *L. cubensis* (western Cuba, Isla de Pinos), *L. protensa* (Hispaniola, discussed above), *L. herminieri* (Guadeloupe) and *L. quadrangularis* ssp. *antillensis* (Puerto Rico to Grenada, but also on the Paraguaná-Peninsula, Venezuela). Even the number of more widespread forms occurring in this area is small; only *L. lancea* var. *lancea* is found almost throughout. *L. stricta* (3 varieties) and *L. portoricensis* are restricted to the Greater Antilles, *L. arcuata* to Cuba and Hispaniola, and *L. quadrangularis* ssp. *subalata* to Cuba. With the possible exception of the latter these forms are probably of South American origin, as the greater parts of their areas and their relatives are found there. They probably reached Central America not earlier than late Miocene times when the mainly volcanic land connection between Colombia and Nicaragua is believed to have come into existence (an earlier, Mesozoic connection is probably of no importance for the species under consideration). In the same period, and well into the Pliocene, Jamaica and Hispaniola were connected with Honduras—Nicaragua. The few continental forms of these islands may be assumed to have reached them in this era. Cuba was already isolated at that time, but it is not very difficult to imagine that the continental species of eastern Cuba arrived there from closely adjacent Hispaniola or Jamaica without the help of a land connection. *L. quadrangularis* ssp. *subalata*, known from eastern Cuba but neither from Hispaniola nor from Jamaica, will perhaps eventually be discovered on the former island or on both. Immediately the question arises why only a few very widespread species occur in Jamaica but none of the Andean or Central American forms found in Hispaniola and/or Cuba, whereas Jamaica must have served as a stepping-stone if a land bridge was of any importance for their dispersion. This is even much more striking when we turn to other ferns. Numerous examples of this type of distribution, i.e. occurring in Hispaniola but nowhere else in the West Indies, were given by CHRISTENSEN (1937, p. 4). Here only the examples of the genera *Phanerophlebia* and *Phyllitis* may be cited, each of which has one species in Hispaniola only, on none of the other islands, but is represented in Central America and/or Mexico. The following solution for this problem is suggested. In Miocene and Pliocene times, when the immigration to these islands may be supposed to have taken place, the mountains of Jamaica are believed to have reached much higher elevations than at present (SCHUCHERT, p. 416), but by subsequent erosion and subsidence became later again considerably lower. Many of the continental (montane) forms must then have disappeared from Jamaica but remained in Hispaniola where to-day the highest elevations of all West Indian islands are found. This explanation does not fit all species with such a gap in their distribution; *L. quadrangularis* ssp. *subalata*, for instance, occurs in Central America at elevations well within the range of the mountains of Jamaica. Besides, it should be pointed out that Jamaica still has a considerable proportion of continental elements in its fern-flora, many of which reach Hispaniola and/or eastern Cuba.

The geological history of western Cuba is quite independent from the East, the general vegetation is quite different, and it is not astonishing that only *L. portoricensis* occurs there (although *L. stricta* might also be expected), besides the strange endemic *L. cubensis*. As the taxonomic position of this fern is not known with sufficient certainty, it is preferable not to speculate about the geological-paleogeographical backgrounds of its distribution; the only species which is probably related is *L. linearis* from Australia, New Zealand, and New Caledonia.

It seems to the author that the distribution of the species discussed above which occur on the Greater Antilles and on the continent can be much better explained by the assumption of a tertiary land-connection between Central America and those islands than by explaining their presence through dispersal of diaspores across the sea (waif-arrivals). This was done by BEARD, who did not believe in any former land-connection in this area.

On the other hand, the poverty in widespread and in endemic species of the Lesser Antilles is in good accordance with their volcanic origin (with few exceptions for islands that are of no interest here), without any land-connection throughout their history. It seems feasible that *L. divaricata* (Guadeloupe), *L. guianensis* ssp. *guianensis* (Guadeloupe, Martinique, Grenada), and *Ormoloma imrayanum* (Guadeloupe, Dominica) came from the adjacent mainland by wind-borne spores; *L. quadrangularis* ssp. *antillensis* may have come from Puerto Rico, or may be a locally developed species. *L. herminieri*, the only endemic of the Lesser Antilles in the genus, is restricted to Guadeloupe, which belongs to the central, probably oldest (Miocene) group of islands.

This demonstrates again that the widespread belief in easy dispersal of viable fern-spores across great distances of lowlands or sea is not generally true. Otherwise it is difficult to explain why at least eight taxa migrated across the land-bridge between Colombia and Nicaragua, whereas at most half that many are distributed over northern South America and the Lesser Antilles. In this connection it is remarkable that Trinidad, which is botanically and geologically part of South America, and is very close to it, possesses but six or possibly seven forms of *Lindsaea*. All of them occur in adjacent Guayana.

The preponderance of Guayana in terms of concentration of species (endemics and non-endemics) is very outstanding. The explorations of the Guayana Highlands, begun by Humboldt & Bonpland, Spruce, the Schomburgk-brothers, Appun, and others, recently resumed by Ll. Williams, Schultes, Cabrera, and especially by Steyermark and by Maguire and his collaborators, have revealed the presence of a wealth of interesting forms, and more may be expected. In the present study, 10 species and varieties are described as new that so far have only been found in that area. This does not mean, of course, that collecting in other regions would not be promising; very little material is extant from the interior of the Brazilian shield (states of Matto Grosso, Goias, western Minas Gerais, etc.); most if it is from von Lützelburg's collections. More or less the same is true for Paraguay, Bolivia, and the Amazonian parts of Ecuador and Perú. Only from the West Indies, most of Central America (except Nicaragua), and the coast of south-eastern Brazil, few new forms or records may be expected.

Exchange of species between the Guiana and the Brazilian shield may have occurred (and still occur) across what is now the mouth of the Amazon river where the gap between them is comparatively narrow. This way may have been followed by *L. pallida* (map 18), *L. stricta* var. *parvula* (map 34), and a number of other ferns which show this type of distribution, such as *Bolbitis macrophylla* and *Doryopteris sagittifolia*. The gap in north-eastern Brazil that cuts the area of some of these species in two more or less separate parts may be due to the drier climate of this area, but it is possible that more intense collecting will reveal the presence of some species, now believed to be discontinuous, in locally suitable habitats. Yet it is unlikely that all floristic discontinuities between Guayana and south-eastern Brazil can be explained in this way. A number of species extend from the Guianas to the South along the eastern slope of the Andes and reappear in south-eastern Brazil, sometimes across Bolivia and Paraguay with hardly any break in their area, others with a considerably discontinuity. TRYON's distribution-maps for the species of *Doryopteris* (1942, 1944) provide excellent examples. While in some instances it may be argued that such species may eventually be found in intermediate localities or may have been present there in former times, this explanation can hardly serve for all these discontinuous patterns of distribution. BRADE (1942), who cited numerous examples of this kind of discontinuity, assumed that the mountains of Matto Grosso and Minas Gerais might have served as stepping-stones; but it is doubtful whether this explanation holds in all cases, particularly for such ferns of higher elevations as *Jamesonia* (Andes from Costa Rica to Bolivia; one endemic species on Mt. Itatiaia, s.e. Brazil). In the author's opinion no satisfactory explanation for this type of distribution has been given. Even more puzzling are the cases where the southern Andes are not included in the area, for example in *Lindsaea quadrangularis* (maps 14—17), and on Tryon's map of *Doryopteris nobilis*.

It is not easy to decide whether both Guayana and Brasilia developed their own more advanced species side by side that later did or did not become more widespread, but this seems quite likely. *L. ovoidea* from south-eastern Brazil, for instance, is probably a local derivative of the section *Pseudosphenomeris*, whereas in Guayana an almost unbroken series from primitive to advanced forms is present, with a gap between the type represented by *L. sphenomeridopsis* and that of the section *Temnolindsaea*, which was probably once bridged by a form analogous to the Brazilian *L. virescens*. It is not possible to ascertain whether *L. filipendula* and the two ssp. of *L. quadrangularis*, endemic in Brasilia, are phyletically connected with autochthonous primitive forms or whether they are derived from more advanced ones that originated elsewhere.

Let us now turn to the distribution of primitive groups and allied genera in order to make an attempt to reconstruct something of the history of the genus and its constituents.

Copeland (1939, p. 179; 1947, p. 53) was convinced that *Lindsaea* is of Antarctic origin, which he believed to be true for about nine-tenths of the living ferns (1947, p. 7). The writer does not believe that in the case of *Lindsaea* the evidence is conclusive.

The section of this genus regarded at the most primitive by the author, at least in the New World, perhaps in the whole genus, is *Pseudosphenomeris*. It has one species in Annam and Hai-nan, one in Madagascar, two in south-eastern Brazil, and one in Venezuela (map 3). This kind of distribution strongly suggests a relic-group, and there is little evidence for linkage with Antarctic or Subantarctic regions. The presence of one species in Indo-China and one in Venezuela cannot be readily explained by the assumption of Antarctic origin. Notably the presence of *L. sphenomeridopsis* in the Upper Orinoco region is very interesting because it presents evidence for the presence of the most primitive section on both tropical South American shields, whereas formerly it was only known from the southern shield, which might have been interpreted as evidence for a southern centre of distribution. But if this section were of Antarctic origin, one would expect it in Chile, New Zealand, and Tasmania. The presence of several species of *Lindsaea* in New Zealand and Australia has been used as an argument in favour of southern origin; but a larger number is found in Japan, but little closer to the equator, and considerably farther from Antarctica. It must be admitted that some Australian and New Zealand species are probably rather primitive (*L. viridis*, *L. microphylla*, *L. trichomanoides* *)), but in the light of the presence of equally or perhaps more primitive forms in the northern hemisphere this does not appear to be of overwhelming significance.

Sphenomeris is another primitive group, as primitive as or perhaps more primitive than *Lindsaea* sect. *Pseudosphenomeris*. A glance at the list on p. 106 where most species correctly referred to *Sphenomeris* are listed, together with their distribution, conveys again the impression that this is a relic-group. There is only one widespread species, the others are scattered through the tropical and, in the New World, also the subtropical regions. The presence of two endemic or subendemic species in New Caledonia may be significant, as on that island other forms occur which are very likely Antarctic elements, e.g. *Nothofagus;* but again, this evidence is not conclusive, as it may well be explained by the very early isolation of New Caledonia where primitive, perhaps formerly more widespread types survive that were elsewhere replaced by more modern forms. There is nothing in the distribution of the three species of *Sphenomeris* in the Western Hemisphere that points to Antarctic origin.

It is a fact that generally the genus *Lindsaea* extends farther southward than northward from the equator, which is also observed in many other groups of ferns (*Cyatheaceae*, *Dicksoniaceae*, *Gleicheniaceae*, etc.), but this is no unambiguous argument pointing to Antarctic provenience. The climate in South Temperate latitudes is in many regions more equable in terms of temperature and precipitation than the more arid or continental climates prevailing in comparable northern latitudes, and supports a greater number of ferns. But this has not necessarily always been the case, and the presence of single representatives of mainly tropical and southern genera in northern regions where they often appear to be relics, e.g. *Schizaea pusilla* and *Lygodium palmatum* in Atlantic North America, *Culcita macrocarpa* on the Iberian Peninsula and in Macaronesia, *Trichomanes* in Atlantic Europe, eastern North America, and the Russian Far East (see KRYSHTOFOVICH, 1935) suggests that it has been different at one time. Fossil evidence for the past distribution of some groups of ferns pointing in the same direction has been summed up by SEWARD (1922). But even if Antarctica was involved in the migration of many recent ferns, it does not follow that it was the cradle of most or any of them. The author believes that with the evidence available at the present time it is impossible to establish the place of origin of *Lindsaea* and *Sphenomeris*, but it seems likely that they had a wide distribution from very early, possibly Mesozoic, times, and evolved in different directions in their two present-day centres, Malaysia/Polynesia, and Tropical America.

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*) Attention is drawn to the fact that the name *L. cuneata* (Forst. f.) C. Chr., 1906, for this well-known species from New Zealand and Australia is illegitimate, as it is a later homonym of *L. cuneata* Willd., 1810. The correct name is *L. trichomanoides* Dryand.

The absence of any endemic and all but one widespread Old World species in continental Africa has probably to be explained by the aridity which is widely believed to have prevailed in most of Africa during geologically rather recent times. Madagascar did not or only partly share this fate and retained an assortment of endemics and widespread, otherwise mainly Asiatic species. It is difficult to say whether *L. ensifolia* reached continental Africa before the arid period and survived locally, or whether it is a more recent immigrant. Its discontinuous distribution and the presence of a related, probably derived species on the other side of the Atlantic (*L. macrophylla*) seems to favour the first assumption; but then the absence of any differences between the West African and the Asiatic specimens of *L. ensifolia* is difficult to understand.

13. ECOLOGY

The great majority of species inhabit moist forests at lower and middle elevations. A few prefer more open habitats: *L. pratensis*, *L. pendula*, *L. schomburgkii*, *L. rigidiuscula*, *L. javitensis*, and *L. stricta*, and two are restricted to forests at middle and higher elevations, above 1000 m, namely, *L. klotzschiana* and *L. arcuata* (the latter not quite throughout its range). The number of euryoecous species is small; the only good example is *L. portoricensis* (p. 221), whereas some forms of *L. stricta* prefer marshes and others forests. None of the neotropical species is essentially epiphytic (some of the Old World representatives have scandent rhizomes), but a few are occasionally reported as growing on moss-covered tree-trunks, notably in western Colombia and south-eastern Brazil. There are few data on the composition of the soil where Lindsaeas grow; specimens that were not collected in the humus of a forest have been reported from sand, igneous or sandstone rocks, swamps, etc. There is little or no relation between habitat and range; two of the most widespread species, *L. lancea* and *L. divaricata*, inhabit forests, the third, *L. stricta*, occurs mostly in exposed situations, and *L. portoricensis* is found in very diverse surroundings.

In *L. stricta* and *L. protensa* the leaf-apex is often absent, and when it is present, it is usually immature, although the rest of the leaf may be fully developed, with mature sori. The leaves seem to develop very slowly, perhaps even intermittently, as in *Jamesonia*. Generally the leaves are probably rather long-lived; epiphyllous Hepatics are often present.

14. Uses

No reference to any use of ferns of the genus *Lindsaea* has been found, except in Seba (1735), who wrote about his "*Adiantum lancea*" (= *Lindsaea L.*): "ses vertus sont pectorales, telles que celles du capillaire de nos climats, dont l'usage si efficace contre la Toux & les autres maladies du poumon, est connu de tout le monde." This may, however, be due to confusion with true species of *Adiantum*. The very small number of vernacular names (recorded in the special part) is probably a reflection of this lack of application of these plants. Santamaria (1942) did not list a single vernacular name for the genus.

B. TAXONOMIC PART

Material

The present revision is based on the study of about 6000 herbarium-sheets, mainly consisting of the material from the following herbaria (standard abbreviations now in general use):

A	The Arnold Arboretum of Harvard University, Cambridge, Mass.
B	Botanisches Museum, Berlin-Dahlem, Germany.
BM	British Museum (Natural History), London, England. (including the herbarium of Carl Christensen cited as C. Chr. in BM)
BR	Jardin Botanique de l'Etat, Bruxelles, Belgium.
C	Botanical Museum & Herbarium, Copenhagen, Denmark.
F	Chicago Natural History Museum, Chicago, Ill.
FI	Herbarium Universitatis Florentinae, Florence, Italy.
G	Conservatoire et Jardin Botaniques, Genève, Switzerland.
GH	The Gray Herbarium of Harvard University, Cambridge, Mass.
GOET	Systematisch-Geobotanisches Institut, Göttingen, Germany.
IA	Department of Botany, State University of Iowa, Iowa City, Ia.
K	The Herbarium, Royal Botanic Gardens, Kew, England.

L	Rijksherbarium, Leiden, Netherlands.
LE	Botanical Institute of the Academy of Sciences, Leningrad, U.S.S.R.
M	Botanische Staatssammlung, München, Germany.
MO	The Missouri Botanical Garden, St. Louis, Mo.
NY	The New York Botanical Garden, New York, N.Y.
PH	The Academy of Natural Sciences, Philadelphia, Pa.
S	Botanical Department, Naturhistoriska Riksmuseum, Stockholm, Sweden.
S-PA	Paleobotaniska Avdelningen, Naturhistoriska Riksmuseum, Stockholm, Sweden.
U	Botanisch Museum & Herbarium, Utrecht, Netherlands.
UC	Herbarium of the University of California, Berkeley, Cal.
UPS	Institute of Systematic Botany, University of Uppsala, Sweden.
US	United States National Herbarium, Smithsonian Institution, Washington, D.C.
W	Naturhistorisches Museum, Wien, Austria.

In addition smaller quantities of material were received for study from the following herbaria:

EAP	Escuela Agricola Panamericana, Tegucigalpa, Honduras.
HBR	Herbario "Barbosa Rodrigues", Itajaí, Santa Catarina, Brazil.
P	Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, France.
PI	Istituto Botanico dell'Università, Pisa, Italy.
Pic.-Ser.	Private herbarium of Prof. Dr. R. E. G. Pichi-Sermolli, Florence, Italy.
RB	Jardim Botánico, Rio de Janeiro, Brazil.
SI	Instituto Botánico "Darwinion", San Isidro, Argentina.
USM	Herbario San Marcos, Museo de Historia Natural, Lima, Perú.

The author wishes to express his deep gratitude to the directors and curators of all these Herbaria who made large quantities of valuable material available to him, often for a considerable time. Furthermore, he is much indebted to Dr D. E. Meyer, Berlin-Dahlem, for sending him photographs of specimens in the Willdenow-Herbarium that could not be sent on loan.

Maps

The distribution-maps have been compiled from the data on the herbarium-labels or in enumerations of specimens where they are sometimes more extensive. No literature-records alone have been used, mainly because of the general unreliability of identifications published in enumerations and floras. The localities were mainly located with the help of the "Index to Map of Hispanic America" (Washington, 1943–44) published by the American Geographic

Society. The author is highly indebted to this Society for sending him a free copy of this most excellent and useful Index. The spelling of the names is generally in accordance with the Index.

Each dot represents one or several closely adjacent localities; those which could only approximately be located are indicated by open circles. Localities of dubious specimens and those which could not be found in the Index or on any map have not been indicated, except in the latter case when the province or country in which they were situated was comparatively small; then a circle has been used. Species known from only one locality have mostly not been mapped. The maps are from Goode's series of base maps, published by the University of Chicago Press.

Key and descriptions

The key to the species of *Lindsaea* offered below is largely artificial, although the sections appear more or less as units. As several species are not constant in characters used in the key which serve to separate others, these forms appear in more than one place. For this reason and because of the fact that in the section *Lindsaea* which contains the bulk of the species the relationships are often not quite clear or appear to be reticulate, it would be practically impossible to construct a key in such a way that each species appears only once and is always closest to its nearest relatives.

It is hoped that perhaps 90 % of the specimens can be keyed out in a satisfactory way. (In most cases it will be difficult or impossible to determine sterile or incompletely fertile and immature specimens, although these can not rarely be named by an expert well acquainted with all species). For the remaining 10 %, where certain characters used in the key will be found to be aberrant, the descriptions and figures will have to be consulted in the first place. For this reason almost every taxon has been figured, and the descriptions are rather detailed, which would be superfluous in a group where one or a combination of a small number of characters serve to separate the species quite unambiguously. The degree of dissection has but rarely been used as a key character, but it is mentioned with all species or species-groups because although it is often unreliable it may sometimes be of importance. In addition the overall distribution has been listed in the key, as this may also help to prevent misidentifications where the characters employed are rather subtle.

Although most characters used in the key can be observed on the abaxial side of the leaves, in some cases the adaxial side should also be accessible for examination. In this connection the author wishes to point out that fern-specimens should never be pasted directly to the sheets, as in most cases, especially in small ferns which are not folded, this renders one of the sides inaccessible. Material mounted in such a way may become quite worthless in extreme cases, and it is most regrettable that in some of the largest herbaria of the world this way of mounting is still in practice.

A few remarks on the terminology have to be made, although for the greater part the terms usually employed in pteridological publications have been used.

The terms "above" and "below" are always used in the sense of distal and proximal with regard to the rhizome. For the upper and lower surfaces of lamina, petiole, etc., the terms "adaxial" (ventral) and "abaxial" (dorsal) have been used consistently. The word pinnule always applies to a free ultimate segment, regardless of whether the leaf is pinnate, bipinnate, or tripinnate (see p. 128), except in *Lindsaea macrophylla* and *Ormoloma*, where the large symmetric ultimate divisions are presumably homologous to primary pinnae. A segment is a more or less, but not completely, free division (sometimes used in a general way to indicate any kind of ultimate division). When describing the dissection of laminae which are once or several times pinnately divided and then incompletely incised, the terms bipinnate + bipinnatifid, etc., have been used, instead of bipinnate-bipinnatifid, as is usually done, because the latter expression might be misunderstood to mean bipinnate passing into bipinnatifid.

Measurements of pinnules etc. apply to the largest specimens found on a single lamina, unless otherwise stated. The width of more than simply pinnate laminae has mostly not been given, as it is often not readily measured, apices of pinnae being frequently lost or bent to fit collectors' presses or small herbarium-sheets. The general shape of more than simply pinnate laminae depends strongly on the number of primary pinnae, which in most species is quite variable, and therefore has likewise not been described in most cases.

The citations of literature with the synonyms have been restricted to the principal and most readily accessible publications. Because of the widespread misinterpretation of many species there would be little use in endeavouring to give an almost complete list of citations.

KEY TO THE NEW WORLD GENERA OF LINDSAEOIDS

1. a. Leaves scandent, indeterminate, at least tripinnate, the axes often spiny; sori uninerval . . . . 2. *Odontosoria*
   b. Leaves not scandent, determinate, variously incised or simple, never spiny; mostly at least some of the sori borne on more than one vein 2

2. a. Ultimate divisions cuneate, linear, or spathulate; sori uni- or binerval (rarely on more veins); leaves decompound . . 3
   b. Ultimate divisions dimidiate or equilateral, in the latter case not cuneate or spathulate; leaves rarely decompound, mostly bipinnate, pinnate, or simple, rarely (sub)tripinnate. 4

3. a. Indusia attached by the base and part of the sides; scales narrowly lanceolate, the largest in some species over 5 mm long, or, if shorter, of one row of cells throughout or almost throughout; sporangia large, over 200 μ, mostly over 300 μ 1. *Sphenomeris*

b. Indusia attached by their bases only; scales lanceolate, not over 1.5 mm long, the larger ones never of one row of cells only; sporangia with few exceptions below 200 μ in length, never much larger . . . . 3. *Lindsaea*

4. a. Ultimate divisions dimidiate, or, if equal-sided, with continuous sori . . . . 3. *Lindsaea*
b. Ultimate divisions equal-sided; sori uninerval 4. *Ormoloma*

1. SPENOMERIS

Sphenomeris Maxon, Journ. Wash. Acad. Sci. 3: 144 (1913).

Rhizome creeping, mostly with a Lindsaeoid protostele, in a few species reported to be solenostelic. Scales narrowly lanceolate to linear, either with a long subulate apex consisting of one row of cells only, or of one row of cells throughout or almost throughout. Leaves rather close to close, ± distichous, decompound. Ultimate segments linear, cuneate, or spathulate. Sori terminal on one to four veins; indusium fixed at the base and at least part of the sides, opening outwardly; sporangia over 200 μ, mostly over 300 μ long, often few per sorus, mixed with paraphyses (always?); spores monolete or trilete. About 10 species in tropical and subtropical regions of both hemispheres.

Type species: *Sphenomeris clavata* (L.) Maxon (*Adiantum clavatum* L.)
Key to the American species:

1″. Sori of larger segments occupying more than one vein; scales linear, consisting of one row of cells throughout or almost throughout . . . . 1. *S. clavata* (Florida, Greater Antilles)
1′. Sori occupying one vein; scales lanceolate, with at least two rows of cells at the base
  2″. Ultimate segments spathulate, 1½—2 mm wide near the apex . . . . .2. *S. spathulata* (Colombia)
  2′. Ultimate segments linear or slightly cuneate, not over 1 mm wide . . . . 3. *S. killipii* (Colombia)

1. **Sphenomeris clavata** (L.) Maxon, Journ. Wash. Acad. Sci. 3:144 (1913).

Basionym: *Adiantum clavatum* L., Spec. Plant. 2:1096 (1753).
Homotypic synonyms: *Davallia clavata* (L.) J. E. Smith, Mém. Acad. Roy. Turin 5:415 (1793).

Stenoloma clavatum (L.) Fée, Gen Fil. 330 (1852).
Odontosoria clavata (L.) J. Smith, Hist. Fil. 264 (1875).

It is not necessary to describe this well-known species here. A good illustration was given by SMALL (1938, p. 318). Its range (map 4) is: Southern Florida, Bahamas, and Greater Antilles. In Florida, it is restricted to the extreme South; for a long time it was only known from the Everglade Keys (Dade County), but it was recently (March 1952) discovered in the Florida Keys (Monroe County): Big Pine Key, Killip 41421, 42001 (US). In Cuba it is apparently uncommon, except in the East, where it seems to be plentiful; also on Isla de Pinos; otherwise Jamaica, Hispaniola (both Haiti and San Domingo), western Puerto Rico, and Bahamas: islands of New Providence, Andros, Eleuthera, Rose, and Great Abaco.

In Florida, this species occurs in lime-sinks, limestone outcrops and walls of sinkholes in pinelands, also, but rarely, in hammocks (see SMALL, 1920, 1938, CORRELL, 1938, BROUN, 1938). In the West Indies, its habitats seem to be more diverse; it has often been collected on precipitous cliffs, in crevices of calcareous or serpentine rocks, along streams, etc.

The rhizome-scales are up to 2½ mm long, rather dark brown, and consist of one or occasionally at the extreme base of two rows of cells. The sporangia are small for the genus, ca. 220—170 μ, the annulus with 15–17 indurated cells that reach the stalk; spores rather dark brown, trilete, subglobose, ca. 50 × 45 μ. For a figure of the spores, see WAGNER (1952 b, pl. 5 c).

2. **Sphenomeris spathulata** (Maxon) Kramer, comb. nov.

Basionym: *Lindsaea* (?) *spathulata* Maxon, Contr. Gray Herb. 165:74 (1947).

There is little to add to Maxon's very complete description. The scales are very narrowly lanceolate and consist of 2 or 3 rows of cells at the base. The head of the sporangium is ca. 320 × 250 μ, with an annulus with 16—18 indurated cells that do not quite reach the stalk; the spores are trilete, subglobose, pale brown, ca. 46 × 37 μ, probably 32 per sporangium. Type: Haught 1960 (US), from Cerro Armas, dept. Santander, Colombia.

3. **Sphenomeris killipii** (Maxon) Kramer, comb. nov.

Basionym: *Lindsaea* (?) *killipii* Maxon, Contr. Gray Herb. 165:74 (1947).

As in the preceding species, the reader is referred to Maxon's description, to which the following data may be added: scales lanceolate, long-acuminate, with up to 7 rows of cells at the base. Sporangia ca. 330 × 250 μ, annulus with 18—20 indurated cells that do not quite reach the stalk; spores trilete, subglobose, medium brown, ca. 46 × 42 μ.

Type: Killip 7947 (US), from La Gallera in the Micay Valley, dept. Cauca, Colombia.

It is difficult to understand why Maxon included these two species in *Lindsaea*, though with a ?. He commented himself on the resemblance to certain species of *Sphenomeris*, but excluded them from that genus because it had "diplanate spores, and the truly marginal sori are endophyllous and urceolate, with both valves of the indusium similar in texture . . ." (l.c.p. 75). The second statement is not generally true and the first one is very strange, as *S. clavata*, chosen by Maxon himself as type species, has trilete spores.

2. ODONTOSORIA

Odontosoria (Presl) Fée, Gen. Fil. 325 (1852).

Type species: *Odontosoria uncinella* (Kze.) Fée (*Davallia uncinella* Kunze).

For this genus, the reader is referred to Maxon's excellent revision (1913), to which little remains to be added. It seems somewhat doubtful whether *O. wrightiana* Maxon is more than a local form of *O. aculeata* (L.) J. Smith; there are several intermediates, some of them duplicates of specimens cited by Maxon with the type.

Otherwise, there are a few range-extensions which will perhaps be dealt with elsewhere.

3. LINDSAEA

Lindsaea Dryander in J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:401 (1793); Dryander, Trans. Linn. Soc. 3:39 (1797); Roem. Arch. 2 (II): 234 (1801); Swartz, Syn. Fil.x, 5 (1806); Schkuhr, Krypt. Gew. I: 105 (1809); Poiret in Lamarck, Encycl. Suppl. I: 133 (1810); Willdenow, Spec. Pl. V:420 (1810); Poiret in Lamarck, Encycl. Suppl. III:447 (1813); Kunth in H.B.K., Nov. Gen. Spec. I:18 (1815); Kaulfuss, Enum. 218 (1824); Sprengel, Syst. Veget. IV: 79 (1827); Desvaux, Prod. 171 (1827); Sprengel, Gen. Pl. 9th ed. 723 (1830); Presl, Tent. Pterid. 131 (1836); J. Smith, Jo. Bot. 25/26: 88 (1841); J. Smith, Lond. Jo. Bot. 1:423 (1842); Hooker & Bauer, Gen. Fil. t. 63 A (1842); Hooker, Spec. Fil. I:203 (1844)*); Kunze, Bot. Zeit. 8:299 (1850); Fée, Gen. Fil. 104 (1852); Mettenius, Fil. Lips 104 (1856); Moore, Ind. Fil. I:39 (1857); Fée, 10e mém. 13 (1865); Ettingshausen, Farnkr. 211 (1865); Fée, 11e mém. 15 (1866); Bommer Monog. Cl. Foug. 69 (1867); Hooker & Baker, Syn. Fil. 1st ed. 104 (1868), 2nd ed. 104, app. 471 (1874); Fée, Crypt. vasc. Brés. I:29 (1869) Baker, Fl. Bras. I^2: 349 (1870); J. Smith, Hist. Fil. 267 (1875); O. Kuntze, Rev. Gen. Pl. 815 (1891); Sodiro, Crypt. Vasc. Quit. 56 (1893); Christ, Farnkr. d. E. 291 (1897); Jenman, W. Ind. Gui. F. 70 (1899); Diels, N. Pfl. I^4: 219 (1902); Duss. Fl. Crypt. Ant. franç. 58 (1904); Maxon, Pter. Port. 488 (1926); Pérez Arbeláez, Bot. Abh. Goebel 14:53 (1928); Posthumus, Fl. Surin. Suppl. 68 (1928); Domin, Pterid. Domin. 242 (1929); Copeland, Univ. Calif. Publ. Bot. 16 (2): 83 (1929); C. Christensen in Verdoorn, Man. Pterid. 538 (1938); Dutra, An. Prim. Reun. Sul-Am. Bot. II:29 (1938); Capurro, ibid., 106 (1938); Copeland, Gen. Fil. 52 (1947); Hodge, Lloydia 17 (2):102 (1954).

Schizoloma Gaudichaud; Presl, Tent. Pterid. 132 (1836), in part; Hooker & Bauer, Gen. Fil. t. 63 B (1842); Fée, Gen. Fil. 108 (1852), in part; Diels, N. Pfl. I^4:218 (1902), in part; and of other authors.

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*) The year of publication of vol. I of Hooker's Species Filicum is given by Christensen (Ind. Fil.) as 1844 for p. 1–128, for the rest as 1846, probably on the base of Kunze's critical notes in Bot. Zeit. (1844–1850). But Klotzsch in 1844 (Linnaea 18:544) referred already to *Davallia imrayana* as published in Spec. Fil. I: 171, which must have been issued at least up to that page in 1844.

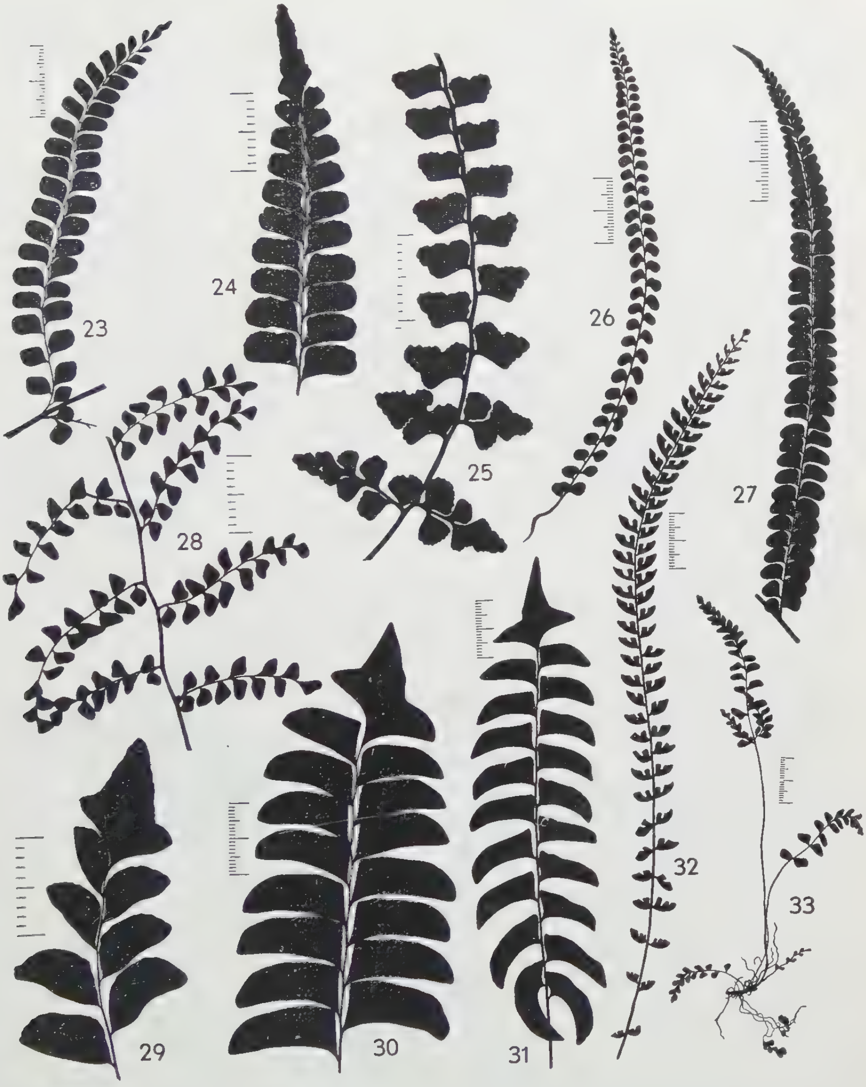

Fig. 23: *Lindsaea ovoidea;* rachis and pinna from middle of lamina (Wacket 167). Fig. 24: *L. portoricensis;* apex of lateral pinna (Focke 913). Fig. 25: *Odontosoria uncinella;* upper part of primary pinna (Howard 6129). Fig. 26: *Lindsaea stricta* var. *stricta;* complete leaf (Glaziou 15722). Fig. 27: *L. guianensis* ssp. *guianensis;* middle pinna (Hostmann & Kappler s.n.). Fig. 28: *L. tenuis;* part of lamina (Schomburgk 1185). Fig. 29: *L. lancea* var. *remota;* apex of simply pinnate lamina (Lanjouw & Lindeman 516). Fig. 30: *L. lancea* var. *falcata;* upper ⅔ of lamina (Sagot 734). Fig. 31: *L. lancea* var. *leprieurii;* lamina (Kappler 1353). Fig. 32: *L. seemannii;* complete lamina (Seemann 976). Fig. 33: *L. cubensis;* complete plant with two fertile leaves (Wright 3947). (Scales in mm).

Davallia J. E. Smith; Sprengel, Syst. Veget. IV: 18 (1827), in part; Presl, Tent. Pterid. 129 (1836), in part; Hooker, Spec. Fil. I: 151 (1844); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 88, in part; Baker, Fl. Bras. I^2: 343 in part; and of other authors.

Odontosoria Fée; Diels, N. Pfl. I^4: 215 (1902), in part; and of other authors.

*) Rhizome creeping or slightly ascending, with a Lindsaeoid protostele. Scales ovate to lanceolate, mostly evenly dark brown, hardly ever clathrate, mostly intermingled with reduced ± hair-like ones. Leaves close to rather remote, inserted in a single row or subdistichous. Petiole stramineous to blackish, always dark at the base. Lamina decompound, three times to once pinnate or simple; ultimate divisions very variable, mostly dimidiate. Sori terminal on the veins (rarely slightly extending along the vein-ends, oblique) or on a vascular commissure connecting two to all veins of a pinnule or of the whole lamina. Indusium semi-ovate to linear, fixed at its base and, if it is elongate, often at part of its sides, opening outwardly; sporangia numerous, the head mostly between 120 and 200 μ long, rarely slightly over 200 μ; annulus with 7–15 indurated cells which mostly reach the stalk; spores trilete or less often monolete, probably 16 or 32 per sporangium.

Over 200 species in tropical and warm-temperate regions of both hemispheres (map 1).

Type species: *L. trapeziformis* Dryander (= *L. lancea* (L.) Bedd.). (See p. 137).

The genus was named after John Lindsay, a Jamaican botanist who died in 1803. KAULFUSS (1824) changed the spelling to *Lindsaya*, in which he was followed by most subsequent authors, but, as COPELAND pointed out (1947, p. 53), the original spelling *Lindsaea* must be retained, and may be regarded as admissible latinization of an English name.

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*) Description chiefly based on the American species.

KEY TO THE SPECIES

(The number of dashes indicates the number of alternatives; for instance, 1″ means that the key is dichotomous, 2‴ that it is trichotomous under that number, etc.).

1″. Ultimate divisions approximately equilateral, oblong, with anastomosing veins; sori continuous; leaves simply pinnate . . 45. *L. macrophylla* (n.e. South America)
1′. Ultimate divisions cuneate or dimidiate, rarely almost equilateral, or leaves simple; veins, apart from the receptacle, free.
  2‴. Leaves simple.
    3″. Petiole abaxially terete throughout or with short, irregular angles below the apex; spores trilete.
      4″. Lamina with an acumen at the apex; a central main vein present, from which lateral veins depart in a not truly dichotomous way . . . . . 38. *L. sagittata* (Guayana)
      4′. Apex of the lamina rounded; all veins evenly dichotomous. 39. *L. reniformis* (Guayana)
    3′. Petiole abaxially angular above up to the sclerotic patch at the base of the lamina; spores monolete . . . . 40. *L. cyclophylla* (Guayana)
  2″. Leaves simply pinnate, the pinnules downwards gradually reduced and more widely spaced; rachis abaxially terete or keeled; spores monolete.
      5″. Scales clathrate; pinnules incised, sori interrupted . . 42. *L. seemannii* (Panamá, Colombia)
      5′. Scales not clathrate; pinnules mostly entire with continuous sori.
        6″. Pinnules small, the middle ones 5–8 × 3–5 mm, 80–100 to a side, herbaceous; abaxial side of the petiole narrowed-rounded. . . . . 44. *L. protensa* (Hispaniola)
        6′. Pinnules larger, 8–13 × 5–8 mm, 30–50 to a side, coriaceous; abaxial side of the petiole keeled . . . 43. *L. pratensis* (Costa Rica)
  2′. Leaves simply pinnate to tripinnate; when simply pinnate, the lower pinnules never gradually reduced, rarely slightly more apart; spores with few exceptions trilete.
          7″. Secondary pinnae or pinnules pendulous.
            8‴. Pinnules cleft; leaves often subtripinnate to tripinnate, the upper pinnae gradually reduced, the leaf-apex gradually simpler in structure. . . 4. *L. meifolia* (w. Guayana)
            8.″ Pinnules simple; leaves bipinnate with an odd terminal pinna; a few shortened upper pinnae may be present. 5. *L. pendula* (w. Guayana)
            8′. Lower pinnules cleft, upper ones simple, as in the preceding species; lamina rather suddenly contracted below the terminal pinna (a hybrid of nrs. 4 and 5) . . . . . . 6. *L.* × *dissecta*

18′. Axes not winged.

19″. Pinnules 3 × as long as wide, narrowed to the subacute apex; axes stramineous to medium brown; bipinnate . . 8. *L. cultriformis* (n.w. S. America)

19′. Pinnules less than 3 × as long as wide, little or not narrowed at the obtuse, truncate, or broadly rounded apex; axes dark reddish-brown to blackish.

20″. Largest (basal) pinnules decurved and flabellate-widened towards the apex, the base of the lower margin sterile, concave; almost always simply pinnate . . . . 13. *L. botrychioides* (s.e. Brazil)

20′. Pinnules not flabellate-widened towards the apex, the lower ones not decurved; the whole lower margin sterile, straight or convex; almost always bipinnate.

21″. Sori, except in strongly reduced pinnules, regularly interrupted . . . . 7. *L. klotzschiana* (C. and n.w. S. America)

21′. Sori only in some of the largest pinnules with one interruption in the outer and one or two in the upper margin . . . . 12. *L. ovoidea* (s.e. Brazil)

13′. Sori continuous (in completely fertile leaves).

22″. Leavesmostly simply pinnate, somewhat dimorphous, the fertile ones surpassing the sterile ones which are always present; spores monolete . . . . 41. *L. cubensis* (Cuba, Isla de Pinos)

22′. Leaves pinnate to tripinnate, not dimorphous, but often the sterile ones with slightly incised margins; in most species completely sterile leaves rarely found on mature rhizomes; spores with few exceptions trilete.

23″. Petiole abaxially terete throughout.

24″. Petiole reddish-brown to blackish or atropurpureous.

25″. Petiole very slender, wiry, 0.3–0.6 mm in diam.

26″. Indusium ca. 0.5 mm wide; pinnules 4–6 × 2–3 mm; upper margin minutely erose to subentire in fertile pinnules; bipinnate . . . 31. *L. tenuis* (Guayana)

26′. Indusium 1–1 ½ mm wide; pinnules 6–7 × 4–5 mm; upper margin irregularly erose-lacerate in fertile pinnules; pinnate or bipinnate . . . . 30. *L. filipendula* (c. and s.e. Brazil)

25′. Petiole stouter.

27‴. Primary rachis adaxially and secondary rachises on both sides (rarely only abaxially) with pale lateral wings; pinnules obtuse . . 23. *L. divaricata* (widespread)

7.′ Secondary pinnae or pinnules not pendulous.

9″. Leaves more than once pinnate; upper primary pinnae gradually reduced in size and complexity, no conform terminal pinna present; ultimate divisions cuneate or linear, or, if dimidiate, incised.

10″. Ultimate segments dichotomous-divaricate, cuneate or linear, the largest not over 0.8 mm wide at the base; sori mostly uninerval.

11″. Sori of large, broad segments often oblique; colour dull olivaceous in dry specimens . . . . 2. *L. sphenomeridopsis* (Venezuela)

11′. Sori practically always at right angles with the veins; colour vivid green in dry specimens . . . . 1. *L. bifida* (e. Brazil)

10′. Ultimate segments consisting of dimidiate, incised pinnules, their largest lobes at the base up to 2 mm wide, mostly but little divaricate; most sori bi- to quadrinerval . . . . . 3. *L. virescens* (s.e. Brazil)

9′. Leaves simply pinnate, or, if more dissected, with a conform terminal pinna, the upper pinnae not strongly reduced.

12″. Pinnules only with a short basal dimidiate portion, consisting mainly of an obliquely ascending apex with a diagonal midrib, fertile along both sides, 5–7½ × as long as wide; bipinnate. 22. *L. taeniata* (Colombia)

12′. At least the basal half, mostly the whole pinnule dimidiate, or, if the greater part is non-dimidiate, soriferous only along the upper side.

13″. Sori interrupted, mostly separated by incisions of the margin (beware of incompletely fertile pinnules of species with normally continuous sori!).

14″. Most sori uninerval.

15″. Pinnules cleft into narrow oblique lobes, 1.5–2 cm long . . . . 9. *L. stenomeris* (Venezuela)

15′. Pinnules shallowly lobed or subentire, up to 1 cm long . . . . . 11. *L. parkeri* (Guayana)

14′. Most sori at the ends of two or more veins.

16″. Pinnules linear, ca. 10–20 × as long as wide; simply pinnate . . . . 20. *L. dubia* (Guayana, Colombia)

16′. Pinnules relatively much wider.

17″. Pinnules ca. 7 × 3 mm . . . . 11. *L. parkeri* ssp. *steyermarkiana* (Venezuela)

17′. Pinnules larger.

18″. Upper part of the petiole, primary and secondary rachises with conspicuous pale wings along the four edges; mostly bipinnate . . . . 10. *L. tetraptera* (n.w. S. America)

27″. Primary and secondary rachises adaxially with pale wings; pinnules mostly acute or subacute. 25. *L. hemiptera* (Guayana)

27′. Rachises not winged, or only traces of paler wing-like portions present on the adaxial side of the secondary rachises.

28″. Pinnules coriaceous; veins hidden.

29″. Leaves simply pinnate, or with few (up to 3, rarely 5) pairs of strongly ascending pinnae; margin of pinnules mostly incurved around the sori . . . . 27. *L. stricta* (widespread)

29′. Leaves bipinnate, with 6–15 spreading pinnae to a side; margin of pinnules not incurved around the sori . . . 28. *L. javitensis* (Guayana)

28′. Pinnules thinner in texture, or, if firm, veins evident.

30″. Indusim mostly repand-erose; pinnae strongly ascending; secondary rachises with sharp often paler lateral ridges, these irregularly interrupted towards the base . . . . 27. *L. portoricensis* (widespread).

30′. Indusium entire to minutely erose, rarely more strongly erose; secondary rachises abaxially terete, or with continuous lateral ridges; or leaves simply pinnate.

31″. Upper pinnules gradually reduced, confluent with a small terminal segment.

32″. Spores monolete; bipinnate . . . . 14. *L. quadrangularis* ssp. *quadrangularis* (s.e. Brazil)

32′. Spores trilete; pinnate or bipinnate.

33″. Simply pinnate, the greater part of the rachis abaxially angular. 26. *L. portoricensis* (widespread)

33′. Bipinnate, or, if simply pinnate, the greater part of the rachis abaxially terete.

34‴. Texture coriaceous; secondary rachises abaxially angular almost to the base; bipinnate . . 28. *L. javitensis* (Guayana)

34″. Texture herbaceous; secondary rachises abaxially for a considerable part terete; or simply pinnate . . . . 24. *L. guianensis* ssp. *lanceastrum* (Brazil)

34′. Texture herbaceous; secondary rachises dark, abaxially grooved almost to the base, the borders pale and wing-like; bipinnate . . . 14. *L. quadrangularis* ssp. *subalata* (Cuba, Mexico to Colombia)

31′. Upper pinnules but little reduced, not less than half as long as the lower ones, not or only by a very narrow wing connected with the terminal segment.

35″. Secondary rachises abaxially terete at the base, then gradually angular or sulcate, or rarely angular almost to the base; bipinnate 14. *L. quadrangularis* ssp. *terminalis* (s.e. Brazil, Paraguay)

35′. Secondary rachises abaxially terete at the extreme base, then abruptly grooved; or lamina simply pinnate . . . 32. *L. lancea* (widespread)

24′. Petiole stramineous to pale brown.

36″. Texture coriaceous; veins hidden; pinnate or bipinnate 27. *L. stricta* (widespread)

36′. Texture thinner.

37″. Pinnules not more than 1½ × as long as wide, roundish.

38″. Indusium 0.15 mm wide, entire or minutely erose; pinnules often slightly imbricate; bipinnate or pinnate . . . . . . 24. *L. guianensis* (widespread)

38′. Indusium 0.3–0.5 mm wide, more strongly erose; pinnules mostly not imbricate; bipinnate, rarely simply pinnate or subtripinnate . . . . forms of *L. stricta* (no. 27), mainly from s.e. Brazil

37′. Pinnules at least twice as long as wide.

39″. Sterile margin (mostly present in the apex of the pinna) sharply dentate; indusium strongly and irregularly erose-dentate; spores monolete; bipinnate....15. *L. pallida* (Trinidad, S. America)

39′. Sterile margin entire or crenate, or, if with acute teeth, the indusium not strongly erose.

40″. Pinnules 5–9 × 2–2½ mm; pinnate or bipinnate . . . . 17. *L. spruceana* (Perú)

40′. Pinnules longer and wider.

41″. Secondary rachises abaxially at least for a considerable basal part terete, or leaves simply pinnate. 24. *L. guianensis* (widespread)

41′. Secondary rachises abaxially sulcate to the base or mostly with a short terete portion at base.

42″. Pinnules at least 3 × as long as wide . . 16. *L. arcuata* (widespread)

42′. Pinnules not over 2½ × as long as wide 14. *L. quadrangularis* ssp. *antillensis* (e. Caribbean area)

23′. Petiole abaxially at least near the apex flattened or obtusely to sharply angular.

43″. Veins elevated throughout or for the greater part; texture mostly chartaceous or coriaceous.

44″. Leaves bipinnate, with upwards gradually reduced pinnules and a small terminal segment . . . . 29. *L. rigidiuscula* (n. and c. South America)

44′. Leaves simply pinnate, with a large terminal pinnule.

45″. Pinnules 18–35 mm long, up to 2½ × as long as wide . . 33. *L. schomburgkii* (n. and c. South America)

45′. Pinnules 30–45(–70) mm long, 3–3½(–4) × as long as wide 34. *L. semilunata* (Guayana)

43′. Veins raised at their extreme bases only or wholly immersed, obscure or visible as wrinkles in the leaf-tissue.

46″. Petiole delicate, wiry, up to 0.6 mm in diam., mostly quite dark.

47″. Indusium 1–1½ mm wide, grossly erose-dentate; pinnate or bipinnate . . . 30. *L. filipendula* (c. and s.e. Brazil)

47′. Indusium narrower.

48″. Indusium 0.4 mm wide; pinnules trapeziform to dimidiate-ovate, 4–8 mm wide; almost always bipinnate . . . . 12. *L. ovoidea* (s.e. Brazil)

48′. Indusium ca. 0.2 mm wide; pinnules lanceolate, not over 2.5 mm wide; pinnate or bipinnate . . . . . 17. *L. spruceana* (Perú)

46′. Petiole stouter.

49″. Petiole reddish or brown to blackish, sometimes pale-angled.

50″. Pinnules linear, 10–20 × as long as wide; simply pinnate . . 20. *L. dubia* (Guayana, Colombia)

50′. Pinnules relatively wider, not linear.

51‴. Terminal pinnule large, free, without a distinct apex, the distal margin faintly and evenly convex or sinuous; petiole abaxially for the greater part terete; simply pinnate . . . . . 37. *L. ulei* (Venezuela, n. Brazil)

51″. Terminal pinnule free or almost free, with an obtuse or mostly acute apex.

52″. Largest pinnules flabellately widened towards the apex; practically always simply pinnate 13. *L. botrychioides* (s.e. Brazil)

52′. Largest pinnules not flabellately widened towards the apex; once or twice pinnate.

53″. Pinnules narrowed towards the apex, mostly lanceolate; no distinct outer margin developed.

54″. Pinnules lanceolate, 5–6 × as long as wide.

55″. Apex of pinnules acute or shortly acuminate; pinnate, rarely bipinnate 19. *L. surinamensis* (Guayana)

55.′ Apex of pinnules long-acuminate, upturned in the upper ones; bipinnate 18. *L. coarctata* (n.w. S. America, s.e. Brazil)

54′. Pinnules trapeziform to dimidiate-elliptic or oval, ca. 2–2½ × as long as wide: see 53′

53′. Pinnules hardly or not narrowed towards the apex, a distinct outer margin mostly present.
  56″. Secondary rachises abaxially gradually passing from a terete into an angular shape or angular close to base; bipinnate . . . . 14. *L. quadrangularis* ssp. *terminalis* (s.e. Brazil, Paraguay)
  56′. Secondary rachises abaxially sulcate, the groove abruptly starting just above the base; or leaves simply pinnate . . 32. *L. lancea* (widespread)

51′. Upper pinnules gradually confluent into a small terminal segment.
  57″. Largest pinnules 5– more than 6 × as long as wide; bipinnate. 18. *L. coarctata* (n.w. S. America, s.e. Brazil)
  57″. Largest pinnules 3–3½ × as long as wide; pinnate or bipinnate . . . . . . 16. *L. arcuata* (widespread)
  57′. Largest pinnules up to 2½ × as long as wide.
    58″. Texture coriaceous; veins hidden; pinnate or bipinnate . . . . . . 27. *L. stricta* (widespread)
    58′. Texture herbaceous to chartaceous; veins evident.
      59″. Largest pinnules flabellate-widened towards the apex; almost always pinnate . . . . 13. *L. botrychioides* (s.e. Brazil)
      59′. Largest pinnules not widened towards the apex.
        60″. Leaves simply pinnate, with reddish petioles, or, if bipinnate, the secondary rachises abaxially angular, the angles irregularly interrupted towards the base . . . . 26. *L. portoricensis* (widespread)
        60′. Leaves bipinnate (rarely simply pinnate, with blackish petioles), the secondary rachises without lateral angles irregularly interrupted at the base.
          61″. Pinnules not narrowed to the apex, or, if narrowed, there broadly rounded and ± ovoid-elliptic . . 12. *L. ovoidea* (s.e. Brazil)
          61′. Pinnules narrowed to the apex, or, if of almost equal width, more elongate . . . . 14. *L. quadrangularis* (widespread)

49′. Petiole stramineous to pale brown, only at the base darker.
  62″. Terminal segment large, free or almost so; upper pinnules not strongly reduced, not less than half as large as the lower ones.
    63″. Apex of at least some of the pinnules prolonged, pointing obliquely upwards, these pinnules with a diagonal main vein; pinnate or bipinnate.
      64″. Inner margin of pinnules divergent from the rachis; upper pinnules but little reduced, terminal segment almost free . . 21. *L. herminieri* (Guadeloupe)

64′. Inner margin of pinnules approximately parallel to the rachis; upper pinnules more strongly reduced, connected with the terminal segment . . . . the caudate form of 16. *L. arcuata*

63′. Apices of pinnules not prolonged, or, if so, without a diagonal main vein.

65″. Pinnules little or not at all narrowed towards the apex which is rounded at the acroscopic, mostly angular at the basiscopic side; pinnate or bipinnate . . . . . . 32. *L. lancea* (widespread)

65′. Pinnules strongly narrowed towards the acute or acuminate, often upturned apex.

66″. Pinnules 3–4 × as long as wide, mostly dark olivaceous to brown in dry specimens; pinnate or rarely bipinnate 35. *L. latifrons* (Perú)

66′. Pinnules 4–6 × as long as wide, usually bright green in dry specimens; simply pinnate . . . . 36. *L. hemiglossa* (Ecuador, Perú)

62′. Terminal segment small, connected by wings with the uppermost of the gradually confluent, strongly reduced upper pinnules.

67″. Apex of pinnules protracted, pointing obliquely upwards . . . . see 64′

67′. Apex of pinnules not protracted.

68″. Pinnules not more than 2½ mm wide; pinnate or bipinnate . . . . 17. *L. spruceana* (Perú)

68′. Pinnules wider.

69″. Spores monolete; indusium strongly and irregularly erose-denticulate; bipinnate . . . . 15. *L. pallida* (Trinidad, S. America)

69′. Spores trilete; indusium mostly not so irregularly erose.

70″. Pinnules 3–3½ × as long as wide; pinnate or bipinnate . . 16. *L. arcuata* (widerspread)

70′. Pinnules less than 3 × as long as wide.

71″. Pinnules not over 8 mm long, roundish-elliptic; veins hidden; pinnate or bipinnate 27. *L. stricta* (widespread)

71′. Pinnules longer, at least 11 mm, more elongate; veins evident.

72″. Apex of pinnules broadly rounded, sometimes narrowed, but not angular at the basiscopic side . . . . 14. *L. quadrangularis* ssp. *antillensis* (e. Caribbean region)

72′. Apex of pinnules angular at the basiscopic side . . . . aberrant forms of 32. *L. lancea*, with strongly reduced upper pinnules and small terminal segment.

Subgenus A. LINDSAEA.

Ultimate segments various, not free and equal-sided with a median main vein; veins free, or, if anastomosing (Asiatic species), pinnules dimidiate, the upper ones gradually reduced.

Type species: *Lindsaea trapeziformis* Dryander (= *L. lancea* (L.) Bedd.).

Sectio I. **Pseudosphenomeris** Kramer, sect. nov.

Lamina decomposita, apice sensim redacta, sine pinna terminali basalibus conformi; segmenta ultima haud pendula, cuneata, sublinearia, vel dimidiata et dissecta; sori uni- vel usque ad quadrinervii, indusio basi solum affixo.

Species typica: *Davallia bifida* Kaulfuss (= *Lindsaea bifida* (Klf.) Mett. ex Kuhn).

This section, the most primitive in the New World and probably in the whole genus, comprises the decompound species with non-pendulous pinnules, with linear or cuneate, ± divaricate segments or with dimidiate, incised pinnules. For the Old World species belonging to this section, see p. 135.

1. **Lindsaea bifida** (Kaulfuss) Mettenius ex Kuhn, Chaetopt. 26 (1882); Schenck, Hedwigia 35:158 (1896); Christ, Farnkr. d. E. 296 (1897). **Fig. 36**

Basionym: *Davallia bifida* Kaulfuss, Enum. 222 (1824); Sprengel, Syst. Veget. IV:121 (1827); Hooker & Greville, Icon. Fil. II t. 238 (1831?); Presl, Tent. Pterid. 129 (1836); Hooker, Spec. Fil. I:188 (1844), incorr. ascribed to Hooker & Greville; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 101; Baker, Fl. Bras. I^2:346 (1870), t. 41 fig. 3; Rosenstock, Hedwigia 43:216 (1904).

Type: Chamisso s.n., from Santa Catarina, Brazil (prob. P, not seen; Isotype in B!).

Homotypic synonyms: *Odontoloma bifidum* (Klf.) Mettenius, Fil. Hort. Lips. 104 (1852).

Acrophorus bifidus (Klf.) Moore, Ind. Fil. II:1 (1857).

Odontosoria bifida (Klf.) J. Smith, Hist. Fil. 264 (1875); Diels, N. Pfl. I^4:215 (1902), fig. 116 D–F; Rosenstock, Hedwigia 43:216 (1904); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:36 (1930); Wagner, Univ. Calif. Publ. Bot. 26 (1) pl. 18d, fig. 24 f (1952).

Stenoloma bifida (Klf.) Fée, Crypt. vasc. Brés. 1:153 (1869).

Heterotypic synonym: *Stenoloma Glaziovi* Fée, Crypt. vasc. Brés. I:153 (1869), pl. 52 fig. 2. Type: Glaziou 2326 from the state of Rio de Janeiro (P!).

Petioles reddish brown to dark castaneous; lamina decompound, thinly herbaceous; ultimate segments narrowly cuneate, dichotomously divaricate; sori uninerval or rarely binerval; indusium ovate, semi-elliptic or slightly horseshoe-shaped, attached only at the base; spores trilete.

Rhizome short-creeping, often with short ascending branches, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 ½ mm long and 0.25 mm wide, with up to 5 rows of cells at the base. *Petioles* close, 10–30 cm long or less in depauperate specimens, in large leaves roughly as long as the lamina, in small ones often shorter, ± shining, the upper part of the adaxial side with a narrow channel bordered by stramineous ridges which become indistinct towards the base where the channel evanesces rather abruptly, the very base terete, abaxially angular or slightly sulcate above, the angles sometimes paler, becoming gradually obsolete towards the base, the lower ½ or $^{1}/_{3}$ obtusely angular or subterete; diameter ½–1 mm at base of lamina. *Lamina* 9–27 cm long, from almost as wide as to half as wide as long, rhombic or ovate in outline, tripinnate + pinnatifid + bifid or tripinnate + bifid, rather dark green on the ventral, paler on the dorsal side. *Primary rachis* similar to the upper part of the petiole, but the dark colour often hardly visible on the adaxial surface where the ridges are quite broad; axillary cushions obsolete or visible as faint swellings near the bases of the lower pinnae. About 5–7 major *primary pinnae* present on each side, the lower ones mostly subopposite, the upper ones alternate and by degrees reduced to form the gradually less compound leaf-top; the finer the dissection of the leaf, the more gradual the transition. The pinnae are short-stalked (1–3 mm), ascending under an angle of ca. 30–50°, the largest 5–13 cm long and 2–8 cm wide, lanceolate, or, when several more highly dissected basal secondary pinnae are present, ovate. Secondary rachises only in basal pinnae of large leaves similar to the primary, otherwise pale, adaxially shallowly grooved, abaxially terete at the base, above flattened, with ± wing-like margins, the upper part often shallowly sulcate. Larger pinnae with 8–15 secondary pinnae to a side, these rather close, often subcontiguous or contiguous, obliquely ascending, alternate, the largest pinnate + pinnatifid + bifid, smaller ones pinnate + bifid, the upper ones bifid and finally simple, denticuliform, connected by a wing with each other and with the often lobed apical segment. Rachises of higher order with more prominent wings and less obvious central strand, gradually passing into the bases of the ultimate segments. *Ultimate segments* ± equally bifid, with divergent lobes and rather broad acute sinuses, narrowest at the bottom of the incision where they are 0.2–0.8 (rarely 0.1) mm wide, broadened to the apex which is 1–1.5 mm wide, outer margin erose in fertile, subentire but often apiculate or emarginate in sterile segments; marginal strand very narrow and inconspicuous, whitish, the basiscopic side of the base adaxially with a short yellowish somewhat revolute thickening that probably represents a trace of dimidiate condition. Length of the ultimate segments varying with the depth of the sinus, commonly about 2–5 mm. Veins simple and median in the segments, (binerval segments rare), somewhat elevated in dry material, their ends in fertile segments adaxially visible as triangular patches below the receptacle. *Sori* with the receptacle surpassing the vein-end in width, mostly convex; indusium pale, subentire or mostly erose-denticulate, 0.5–1.5 mm long, 0.2–0.3 mm wide, not reaching the margin by its own width or less, ± reflexed at full maturity. Sporangia ca. 115–135(–140) × 95–100 μ; annulus with 10-13 indurated cells; spores very pale brown, ca. 20–23 μ.

Distribution: Eastern and south-eastern Brazil (map 5). In moist primary forests, terrestrial or on decaying logs or moss-covered rocks, from 200 to 1400 m.

Representative specimens:

Brazil. Bahia: without loc., Blanchet 310 (L).

Minas Gerais: Caldas, Mosén 4593 (B, BR, K, M, S–PA, UPS); Serra do Cipo, north of Belo Horizonte, M. & R. Foster 608 (GH, US).

Espíritu Santo: Serra da Caparaó, Mexía 4053 (B, BM, C, GH, S, UC, US); ibid., id. 4066 (B, BM, C, F, GH, K, MO, S, U, UC, US).

Rio de Janeiro: Itatiaia, Dusén 677 (S, S–PA, US, W); Serra dos Orgãos, Gardner 155 (BM, FI, K, W); Nova Friburgo, Beyrich s.n. (B, C, GOET, L); near Rio de Janeiro, Miers 131 (B, K); Upper Macahé, Glaziou 2326 (P, Holotype of *Stenoloma glaziovi* Fée: Isotypes in B, BR, C, C. Chr. in BM, K, S); without loc., Glaziou 5254 (B, C, K, S).

São Paulo: Alto da Serra, Estacão Biologica, L. B. Smith 1836 (C, GH, US); Ypiranga, Matta do Governo, Lüderwaldt 1633 (BM, GH); Paranapiacaba, Brade 8373 (UC), Sorocaba, Mosén 3748 (C, S, S–PA, UPS).

PARANÁ: Serra do Mar, Porto de Cima, Dusén 599a (GH); Villa Nova, Annies 146 (S–PA).

SANTA CATARINA: Pilões, Mun. Pelhoça, L. B. Smith 6213 (US); Joinville, Schmalz 136 (F, MO, UC), id. s.n. (Rosenstock-exs. 53) (B, M, S, SI, S–PA, US, W); Blumenau, Ule s.n. (GH); ibid., W. Müller 642 (B); Spitzkopf, Viereck 49 (M); Ilha Santa Catarina, Gaudichaud s.n. (B); ibid., Schenck 31 (B).

Very easily recognized among all species from the New World by the decompound leaves with narrow cuneate ultimate segments and hardly any trace of a dimidiate leaf-pattern; the only species with which it can be confused is *L. sphenomeridopsis* from Venezuela. The differences are discussed under that species. Perhaps even more closely allied is *L. millefolium* (see p. 135) from Madagascar, which differs chiefly by the more extensive atropurpureous colour of the rachis which has more sharply delimited pale wings, especially on the adaxial side. The similarity of these two species was already pointed out by CHRISTENSEN (1932). Less closely allied are *L. eberhardtii* (p. 135) from Annam and Hai-nan and *L. virescens*, particularly the variety *catharinae*, from the same region as *L. bifida*. The differences are discussed under *L. virescens*.

2. **Lindsaea sphenomeridopsis** Kramer, spec nov.

L. bifidae valde affinis; differt statura minore, lamina olivacea, segmentis ultimis linearibus, non ultra circa ½ mm latis, soris maioribus saepe obliquis.

Typus: Spruce 3416, from the Casiquiare R., Amazonas, Venezuela (W).

This species is closely allied to *L. bifida*. As only two specimens have been examined by the writer, the following description has been restricted to the essential points.

Rhizome creeping, ca. 1 mm in diam.; scales small, lanceolate, up to 0.8 mm long and 0.1 mm wide, with up to 3 rows of cells at the base. *Petioles* close, castaneous, 5–11 cm long, adaxially terete below, flattened above, with pale but hardly wing-like borders, abaxially terete or angular above. *Lamina* 6–8 cm long, about as wide, decompound, bipinnate + bipinnatifid or tripinnate + bipinnatifid; primary rachises and secondary rachises at the base castaneous abaxially, otherwise the axes stramineous, abaxially rounded, adaxially with pale, sometimes slightly wing-like borders. *Ultimate segments* 2–5 mm long, ca. ½ mm wide, uni- or less often binerval, unevenly dichotomously joined, one branch stouter, less divergent, and often incised at the apex. Texture thinly herbaceous. Apex of fertile segments crenate-crenulate, less sharply than in *L. bifida*, of sterile segments blunt, entire. *Sori* uni- or binerval, in the latter case often oblique; indusium strongly erose, ca. 0.3 mm wide, attached at the straight or faintly concave base, ± reflexed at full maturity. Sporangia ca. $140 \times 115\,\mu$; spores trilete.

Only known from type-collection (see the cross on map 3).

VENEZUELA. AMAZONAS: ad flumina Casiquiari, Vasiva et Pacimoni [= Yatua], Spruce 3416 (W, HOLOTYPE; Isotype in K).

The Kew sheet bears the additional annotation: "These spec^{ms} were brought by a woman from a Morichal (= Mauritia-grove) a day's journey at the back of Zuirabuena".

The main differences with *L. bifida*, as indicated above, are the olive colour, the linear segments, and the often oblique sori. The smaller, less elongate laminas may prove to be more variable when more material is available. The segments are rather like those of *Sphenomeris clavata*, but much smaller.

The phytogeographic implications of the presence of a member of the section *Pseudosphenomeris* in Guayana are discussed on p. 146.

3. **Lindsaea virescens** Swartz, Kungl. Vet. Akad. Handl. 1817: 53; Kunze, Bot. Zeit. 8:345 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 106; Baker, Fl. Bras. I^2:356 (1870); Kuhn, Chaetopt. 26 (1882); Schenck, Hedwigia 35:158 (1896): Diels, N. Pfl. I^4:221 (1902).

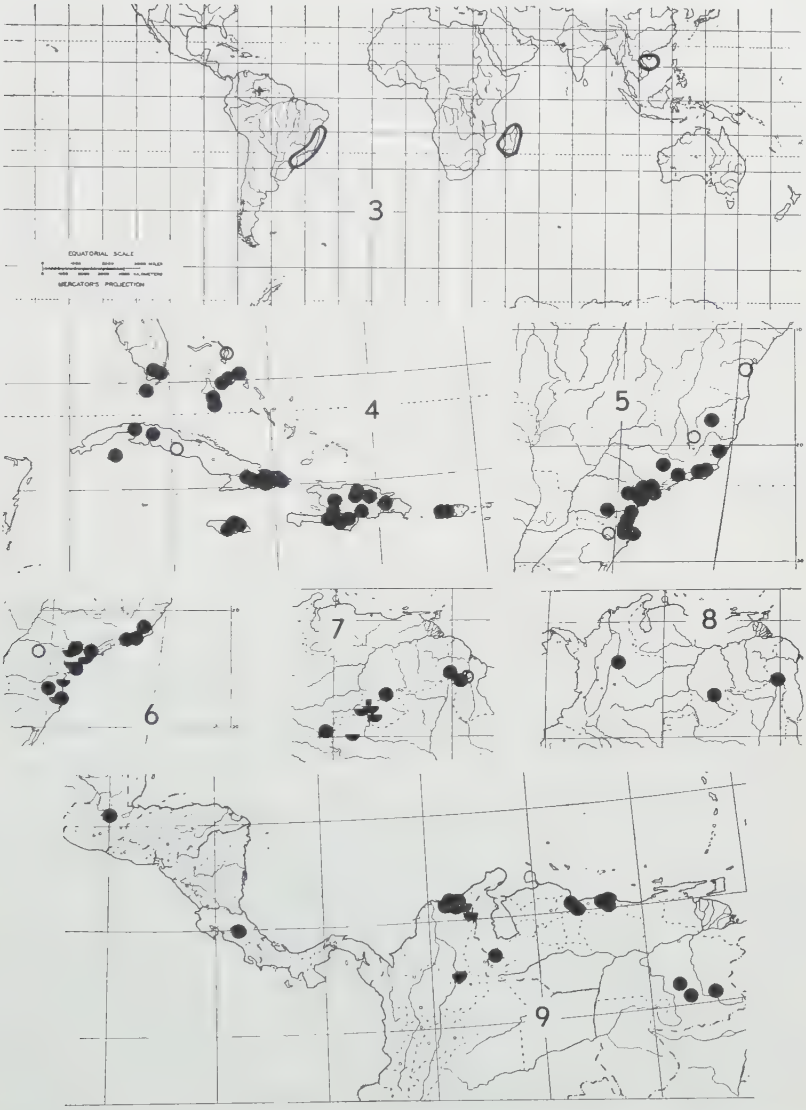
Type: Freyreiss s.n. from Villa Ricca, Brazil (S-PA!).
Homotypic synonyms: *Odontosoria virescens* (Swartz) Rosenstock, Hedwigia 46:79 (1906).
Stenoloma virescens (Swartz) C. Christensen, Ind. Fil. Suppl. III:174 (1934).

Heterotypic synonyms: *Lindsaea genkofolia* St. Hilaire, Voy. Distr. Diam. I:379 (1833). Type: St. Hilaire s.n. from Serra da Piedade, Minas Gerais, Brazil (P!).

Lindsaea Gardneri Hooker, Spec. Fil. I:213 (1844), pl. 65 C; Fée, Crypt. vasc. Brés. I:29 (1869). Type: Gardner s.n. from Serra dos Orgãos, Rio de Janeiro, Brazil (K!).

Petioles reddish brown to dark castaneous; lamina decompound, herbaceous; pinnules dimidiate, ovate to trapeziform, deeply incised; sori mostly bi- to quadrinerval; indusium ovate to linear, attached only at the base; spores trilete.

Rhizome short-creeping, ca. 1–1.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.2 mm long, 0.2 mm wide, with up to ca. 5 rows of cells at the base. *Petioles* very close, about as long as to 1½ × as long as the lamina, ½–1 mm in diam. near the apex, ± shining above, adaxially above with a narrow groove with stramineous lip-like borders, these gradually less distinct below, rather suddenly evanescing near the base which is terete, abaxially angular or slightly sulcate above, the angles paler or concolorous, becoming indistinct downwards, the lower half or one-third bluntly angular, the base, or sometimes also the lower half or third, subterete. *Lamina* 8–ca. 25 cm long, as wide as to $^2/_3$ as wide as long, bipinnate + pinnatifid or bipinnatifid, at the base usually tripinnate + pinnatifid, dark green on the ventral, slightly paler on the dorsal side, dull, rhombic or pentagonal in outline, with 2–5 primary pinnae to a side. *Primary rachis* similar to the upper part of the petiole, adaxially mostly shallowly sulcate with paler margins, abaxially often pale in the upper part. Axillary cushions obsolete or visible as faint swellings at the bases of the lower pinnae. *Primary pinnae* short-stalked (1–3 mm), the upper ones alternate, the lower ones usually subopposite, 7–12 cm long, 1.5–2.5 cm wide, or wider, if pinnate secondary pinnae are present, the upper ones gradually reduced, lower pinnae 1.5–4 cm apart, the upper ones gradually closer, patent under an angle of ca. 30–50°. Secondary rachises adaxially with a green channel bordered by stramineous lips which project laterally and are visible from the abaxial side as narrow green wings continuous with the bases of the pinnules, abaxially mostly stramineous, roundish at the base, flattened or narrowly and shallowly sulcate above; rachises of secondary pinnae similar, with more conspicuous adaxial wing-like margins. Lower primary pinnae with one or two pinnate secondary pinnae on the basiscopic side, rarely also on the acroscopic side, these up to 5 cm long, similar to the upper primary pinnae; sometimes transitions between secondary pinnae and deeply cleft pinnules present. Upper pinnae gradually reduced, the uppermost ones 2–4 cm long, ca. 1 cm wide, finally passing into pinnules, the leaf-top gradually simpler in structure. Ultimate *pinnules* ca. 8–20 to a side in larger pinnae, alternate, subcontiguous to about half their width apart, laxly ascending, the larger ones with a stalk-like base of 1–1½ mm, surprisingly constant in size, 9–12 mm long, 4–6 mm wide, about twice as long as



Map 3: Distribution of *Lindsaea* sect. *Pseudosphenomeris*. Map 4: *Sphenomeris clavata*. Map 5: *Lindsaea bifida*. Map 6: *L. virescens;* complete dots: var. *virescens;* half dots: var. *catharinae*. Map 7: complete dots: *L. pendula;* half dots: *L. meifolia;* square: *L.* × *dissecta*. Map 8: *L. cultriformis*. Map 9: *L. klotzschiana;* complete dots: f. *klotzschiana;* half dots: f. *sublacera*.

wide; transitions between secondary pinnae and pinnules often larger. Lower pinnules hardly or not reduced; axillary pinnule not smaller, but more cuneate in shape. Upper pinnules gradually reduced, more strongly so in the apical part, the uppermost ones denticuliform, 1–2.5 mm long, connected by a wing and confluent with a similar terminal denticule; all lobes up to the extreme apex may be soriferous. Lower margin of pinnules straight or very faintly S-shaped, inner margin straight or ± concave, upper margin in larger pinnules deeply incised, the outer edges of the lobes not in one line, but at small angles with one another. Marginal strand whitish, present throughout, but inconspicuous except at the lower base. Outer margin of pinnules erose-denticulate when fertile, subentire when sterile; quite sterile pinnules rarely observed. Veins immersed but readily visible, (1–)2–4 per lobe, in the latter case the margin often shallowly incised between the members of a pair; main vein not connected with the marginal strand, gradually remote from the lower margin, ca. ½ mm above it near the apex. *Sori* with the receptacle visible adaxially as a fold or wrinkle, laterally extending beyond the vein-ends. Indusium ca. 0.5–3 mm long, 0.2–0.3 mm wide, whitish, subentire to erose-denticulate, not reaching the margin by a distance equalling its width or larger, ± reflexed and conceiled at full maturity. Sporangia ca. 140–160 × 110–120 μ; annulus with 8–13 indurated cells; spores pale brown, ca. 22–28 μ.

Distribution: South-eastern Brazil (map 6). In forests, terrestrial, among rocks, occasionally on moss-covered tree-trunks, up to ca. 1000 m.

a. var. **virescens.** **Fig. 34**

L. catharinae auct. non Hooker; Fée, Crypt. vasc. Brés. I:30 (1869).

Petioles 7–25 cm long; lamina tripinnate mostly at the very base only; lobes of the pinnules close, touching or overlapping; usually one large basal incision in the upper edge, separating a lobe that occupies about half of the pinnule, connected by a wing of ¼–½ mm with the outer lobe which is usually incised again, the inner one often entire. Ultimate lobes of larger pinnules 0.9–1.9 mm wide at the bottom of the sinus. Sori, esp. the basal ones, often quadrinerval.

Representative specimens:

BRAZIL. MINAS GERAIS: Serra da Piedade, St. Hilaire s.n. (P, HOLOTYPE of *L. genkofolia;* Isotype in B); without loc., Freyreiss s.n. (S–PA).

RIO DE JANEIRO: Tijuca, L. B. Smith & Brade 2217 (GH, US); ibid., Dusén 2537 (S–PA), s.n. (S, UPS); Serra dos Orgãos, Gardner s.n. (K, HOLOTYPE of *L. Gardneri*); ibid., Vauthier 668 in part (B, GH); Gardner 156 (BM, FI, G, Isotypes of *L. Gardneri*?); Nova Friburgo, Beyrich s.n. (L); Mt. Corcovado, Vauthier 658 (B, L); ibid., Langsdorff s.n. (BR); without loc., Glaziou 7959 in part (BR, C, K, LE, US); Dusén s.n. (M, S–PA).

SÃO PAULO: Bosque da Saude, Brade 5175 (UC); Iguape, Brade 8258 in part (UC), s.n. (Rosenstock-exs. II 67) (PH); Rio Grande, Wacket 136 (Rosenstock-exs, 180) (B, BM, L, M, S, SI, S–PA, US, W); Matta do Governo, Ypiranga, Lüderwaldt 1629 in part (BM, GH).

PARANÁ: Villa Ricca, Freyreiss s.n. (S–PA, HOLOTYPE).

SANTA CATARINA: Flaggenberg near Desterro, Schenck 32 (B); Isla Santa Catarina, Ule 209 (B).

b. var. **catharinae** (Hooker) Baker, Fl. Bras. I^2:356 (1870) **Fig. 35**

Basionym: *Lindsaea Catharinae* Hooker, Spec. Fil. I:212 (1844), t.65 B.

Homotypic synonym: *Odontosoria virescens* (Swartz) Ros. var. *catharinae* (Hooker) Rosenstock, Hedwigia 46:79 (1906). Type: Beechey s.n. from Santa Catarina, Brazil (K!).

Petioles up to 37 cm long; lamina more fully tripinnate; secondary rachises abaxially occasionally dark; sinuses of the incisions of the pinnules wider, the lobes more divergent; largest pinnules often with 6 distinct lobes; ultimate lobes narrower, 0.6–1.5 mm wide at the bottom of the sinus. The great majority of the sori binerval, quadrinerval ones quite rare. A few giant spores, 42 × 32 μ, found together with normal ones.

Brazil. São Paulo: Matta do Governo, Ypiranga, Lüderwaldt 1629 in part (GH); Iguape, Brade 8258 in part (BM, GH, S–PA, US); Serra do Itatins, Brade 8258a (UC).

Rio de Janeiro: Without loc., Glaziou 2325 (BR, C, K, S).

Santa Catarina: Joinville, Schmalz 161 (F); without loc., Beechey s.n. (K, Holotype).

Although the two varieties occur in the same area and are not rarely collected together, they are usually quite distinct, and intermediates are rare. Very ample material may show in the future that they cannot be maintained, but with the material extant it seems that they can stand as varieties. *L. virescens* can hardly be confused with any other species, except var. *catharinae*, which sometimes approaches *L. bifida*, but that species has mostly uninerval sori, smaller sporangia, and narrower ultimate lobes.

Sectio II. **Crematomeris** Kramer, sect. nov.

Lamina decomposita vel bipinnata, petiolo rhachidibusque abaxialiter teretibus, rhachidibus secundariis angulo fere recto patentibus, basi torquatis, ut facies abaxialis basiscopica, adaxialis acroscopica; segmentis secundariis (pinnulis) deflexis, pendentibus.

Species typica: *Lindsaea pendula* Klotzsch.

This section comprises the two strange species with patent secondary rachises twisted at the base and pendulous secondary segments, *L. pendula* and *L. meifolia*, and their hybrid, described here as new. The morphology of this group is discussed more at length on p. 130/131.

4. **Lindsaea meifolia** (H.B.K.) Mettenius ex Kuhn, Linnaea 36:79 (1869/70); Kuhn, Chaetopt. 26 (1882). **Fig. 41**

Basionym: *Davallia meifolia* H.B.K., Nov. Gen. & Spec I:19 (1815); Sprengel, Syst. Veget. IV:121 (1827); Presl, Tent. Pterid. 129 (1836); Hooker, Spec. Fil. I:189 (1844); Moore, Ind. Fil. 2:297 (1857); Hooker & Baker, Syn. Fil. 2nd ed. append. 470 (1874); prob. not of Presl, Rel. Haenk. I:67 (1825).

Type: "Near Caracas et Chacao", Venezuela, Humboldt & Bonpland s.n. (not seen; Isotype in B!).

Homotypic synonyms: *Odontosoria meifolia* (H.B.K.) C. Chr., Ind. Fil. (164,) 465 (1906); Knuth, Fedde Rep. Beih. 43 (1):30 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:36 (1930).

Stenoloma meifolium (H.B.K.) C. Chr., Ind. Fil. Suppl. III:173 (1934).

Homotypic (?) synonyms: *Darea fumarioides* H. & B. in Willd., Spec. Pl. V:299 (1810).

Caenopteris fumarioides (H. & B. in Willd.) Desvaux, Prod. 268 (1827); not *Lindsaea fumarioides* (Swartz) Mettenius, 1864, which is *Odontosoria* *fumarioides* (Swartz) J. Smith. Type: "Caracas (v.s.)", Humboldt & Bonpland (?), ubi?

Heterotypic synonyms: *Lindsaea Sprucei* Hooker in Hooker & Baker, Syn. Fil. 1st ed. 108 (1868).

Type: Spruce 2988 from San Carlos, Rio Negro, Venezuela (K!). Homotypic synonyms: *Davallia sprucei* (Hooker) Baker, Fl. Bras. I^2:346 (1870).

Odontosoria sprucei (Hooker) Diels, N. Pfl. 1^4:215 (1902).

Stenoloma gratissima Fée, Crypt. vasc. Brés. I: 152 (1869), pl. 52. fig. 1. Type: Spruce 2988, as above (P!).

Petioles stramineous, abaxially terete; lamina decompound, coriaceous; ultimate segments pendulous, the larger ones once or twice cleft; sori mostly binerval; spores trilete.

Rhizome short-creeping, ca. 1.5 mm in diam.; scales lanceolate, acuminate, up to 0.8 mm long, 0.25 mm wide, with up to 8 rows of cells at the base. *Petioles* close, 6–28 cm long, from slightly longer than to twice as long as the lamina, $^3/_4$ mm in diam. near the apex, dull, adaxially sulcate, the groove flat below, broadly and shallowly concave above. *Lamina* bipinnate + pinnatifid to tripinnate + pinnatifid, ovate to lanceolate in outline, olivaceous to rather dark brown, often ± shining, 5–16 cm long, 3–5.5 cm wide. (Lamina of juvenile plants with secund pinnules, deflexed-pendulous on one side). *Primary rachis* similar to the upper part of the petiole. Axillary cushions not seen. *Primary pinnae* ca. 6–15 to a side, the lower ones subopposite, the upper mostly alternate, subsessile, patent under an angle of ca. 90° or the upper ones slightly ascending, their apex often decurved, 1.5–3 cm long, their width very variable depending on the degree of dissection, in the upper half of the lamina gradually, near the apex more suddenly reduced, rarely (in small leaves) gradually shortened from base to apex of lamina, the lower ones 1–1.5 cm apart, the upper ones slightly closer. Secondary rachises terete abaxially, sulcate adaxially, with a torsion at the extreme base, the adaxial side orientated towards the apex, the abaxial side towards the base of the lamina. Lower primary pinnae with one or two, sometimes with more, pairs of pinnate secondary pinnae at their bases, these up to 0.5–1.5 cm long, prob. those of both sides pointing downwards in the natural condition, but in dried specimens sometimes folded out. Ultimate *pinnules* (which are rarely borne directly on the secondary rachises, except in the apical part of the pinnae) bent over 90° in the stalk-like base, narrowly lanceolate, or almost linear and acute when sterile, the lower ones subopposite, the upper ones alternate, ca. 10–15 to a side, 1–2 mm apart, 2–2.5 mm long, the upper ones shorter, ca. 1 mm long, 0.2–0.8 mm wide, the largest twice deeply cleft, the smaller ones once, those in the apical part of the pinnae and in the apical primary pinnae spathulate, entire but for the erose outer margin, resembling those of the next species, intermediates between these extremes not rare. Basiscopic margin of pinnules thickened, stramineous, the other margins less thickened, pale. Apex of lamina gradually simpler in structure, with transitions from short pinnae through strongly incised pinnules to little or not divided pinnules, these deflexed, and also pendulous, as the primary rachis of the leaf-top is bent over to one side. *Sori* mostly binerval; indusium stramineous, rigid, ca. 0.4 mm wide, irregularly erose-denticulate, as the fertile margin, which it equals, more or less bulging at full maturity. Sporangia ca. 230 × 160 μ; annulus with 13-16 indurated cells; spores medium brown, ca. 32–40 μ.

Distribution: Along the north-western border of the Amazon basin; apparently uncommon (map 7). In most forests, up to 300 m.

COLOMBIA. VAUPÉS: Puerto Colombia (opp. Venezuelan Maroa), Río Guainía, Schultes, Baker & Cabrera 18168 (US).

VENEZUELA. AMAZONAS: San Carlos, R. Negro, Spruce 2988 (K, HOLOTYPE of *L. sprucei;* P, HOLOTYPE of *Stenoloma gratissima;* Isotypes in BM, BR, G, GH, W); Maroa, R. Guainía, Ll. Williams 14279 (F, G, US), "near Caracas and Chacao",

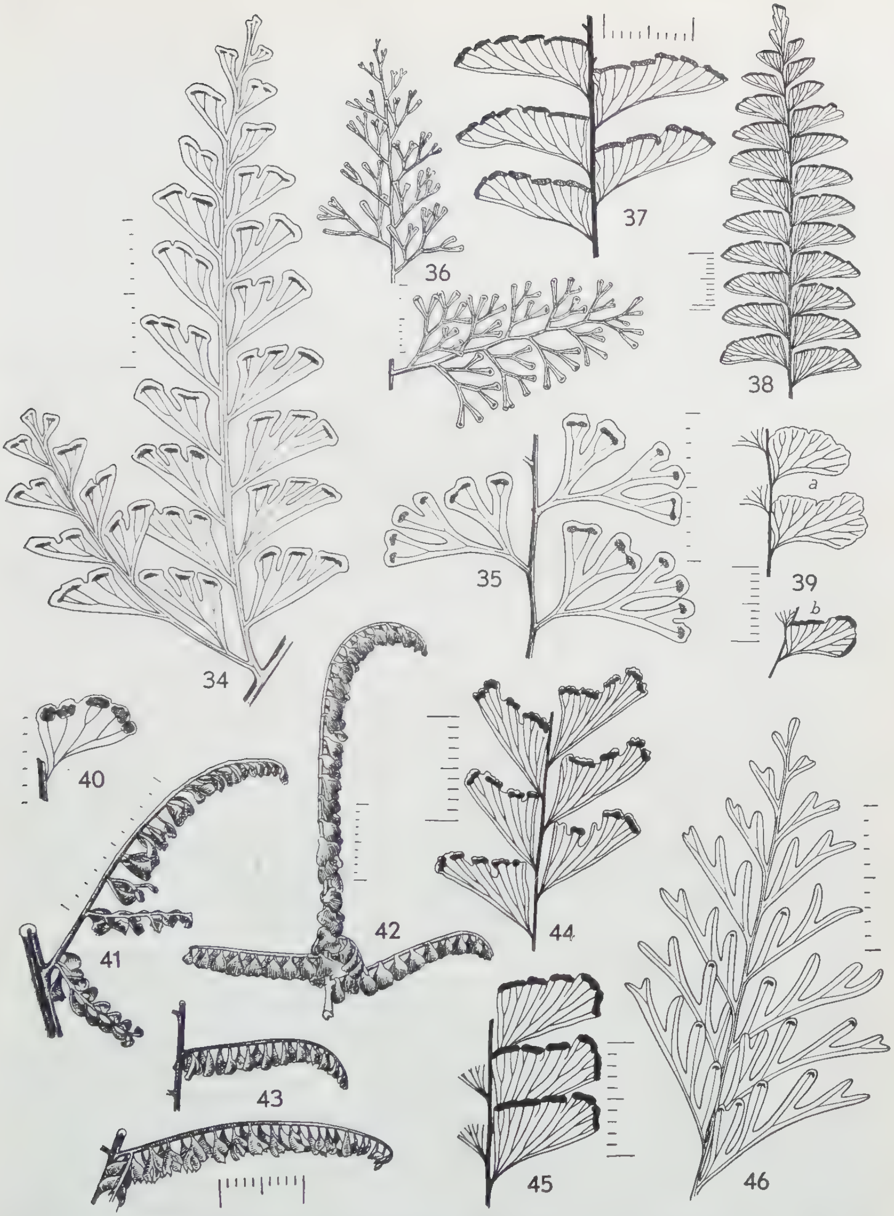


Fig. 34: *Lindsaea virescens* var. *virescens;* middle pinna (Schenck 32). Fig. 35: *L. virescens* var. *catharinae;* pinnules from middle of pinna (Glaziou 2325). Fig. 36: *L. bifida;* apex of lamina (above) and middle pinna (Mendonça 417). Fig. 37: *L. cultriformis;* pinnules from base of terminal pinna (Kalbreyer 1650). Fig. 38: *L. tetraptera;* apex of lateral pinna (Jenman s.n.). Fig. 39: *L. ovoidea;* sterile (a) and fertile (b) pinnules from terminal pinna (Brade 8261). Fig. 40: *L. parkeri* ssp. *parkeri;* pinnule from bipinnate leaf (Sandwith 1391). Fig. 41: *L. meifolia;* middle pinna (v. Lützelburg 23606). Fig. 42: *L. pendula;* apex of lamina (Maguire & Fanshawe 23160). Fig. 43: *L.* × *dissecta;* basal and upper lateral pinna (Ll. Williams 13934). Fig. 44: *L. klotzschiana* f. *sublacera;* pinnules from middle of basal pinna (Haught 3831). Fig. 45: *L. klotzschiana* f. *klotzschiana;* pinnules from base of terminal pinna (H. H. Smith 937). Fig. 46: *L. stenomeris;* apex of pinna (Maguire, Wurdack & Bunting 37365). (Scales in mm).

more probably from southern Venezuela, Humboldt & Bonpland s.n. (B, Isotype). BRAZIL. AMAZONAS: Jutica, Rio Uaupés, von Lützelburg 23606 (M, NY, UC).

A very distinctive species, not likely to be confused with any other species, except *L. pendula*, with which it shares the pendulous pinnules; *L. meifolia* is, however, more dissected, and has a gradually reduced leaf-top. It is surprising that the close relationship of the two species has hardly ever been noted; BAKER (1870) observed the resemblance, but believed it to be only superficial. Most specimens of *L. meifolia* seen by the writer had been wrongly identified as *L. pendula*. *L. meifolia* was incorrectly reported from Panamá by PRESL (1825) and other authors who copied from him; although the author has not seen his specimen, his description "specimen nostrum Humboldtiano duplo majus" points to a different fern, perhaps an *Odontosoria* or a highly dissected *Asplenium*. It is quite unlikely that *L. meifolia* occurs in Panamá.

5. **Lindsaea pendula** Klotzsch, Linnaea 18:548 (1844); Hooker, Spec. Fil. I:213 (1844), pl. 65A; Kunze, Bot. Zeit. 8:346 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 108; Baker, Fl. Bras. I^2:352 (1870); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Christ, Farnkr. d.E. 293 (1897); Jenman, W. Ind. Gui. F. 78 (1899); Christ in Schwacke, Novas Plantas Mineiras II:30 (1900); Diels, N. Pfl. I^4:221 (1902); Posthumus, Fl. Surin. Suppl. 72 (1928); A. C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Fig. 42

Type: Schomburgk 253 in part, British Guiana (B!).

Petioles stramineous to dark reddish brown, abaxially terete; lamina bipinnate with conform terminal pinna, coriaceous; pinnules pendulous, obovate-cuneate, not incised; sori on 3—5 veins; spores trilete.

Rhizome rather long-creeping, 1.5–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.6 mm long, 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* moderately close to close, 11–44 cm long, 1½–3 × (rarely more) as long as the lamina, ¾–1¾, mostly ca. 1 mm in diam. near the apex, dull, adaxially flattened in the lower, sulcate in the upper part. *Lamina* bipinnate (very rarely subtripinnate; simply pinnate on juvenile rhizomes), ovate to lanceolate in outline, yellowish-green to olivaceous or brownish, 4–26 cm long, 4–11 cm wide, from as long as to almost four times as long as wide, truncate at the base, with 3–18 pinnae to a side. *Primary rachis* similar to the upper part of the petiole. Axillary cushions not seen. *Pinnae* subopposite or alternate, subsessile or the terminal short-stalked (ca. ½ cm), patent under an angle of ca. 90°, their apices often decurved, (2–)3–6 cm long, the upper ones shorter, 1–2½ cm, terminal pinna about the size of the lower pinnae or slightly larger, curved to one side, lower pinnae ca. 1–3 cm apart, the upper ones closer. Structure and orientation of the secondary rachises as in the preceding species. *Pinnules* bent over 90° at their narrow stalk-like base, ca. 10–25 to a side, alternate or the lower ones subopposite, sometimes contiguous or slightly imbricate, the basal pinnule (not reduced) usually more or less overlying the rachis, the largest 2–5 mm long, 2–3 mm wide, 2- less than 2½ × as long as wide, asymmetrically obovate, the basiscopic margin mostly more convex than the opposite side, long-cuneate at the base, entire, or the distal margin erose-repand, especially in fertile pinnules, in sterile ones sometimes with an approximately median apiculus, otherwise truncate or slightly convex, all margins thickened, the thickening strongest at the basiscopic edge. Upper pinnae somewhat shortened, but not strongly and gradually, the terminal pinna always distinct, with second, pendulous pinnules. Upper pinnules gradually reduced, the uppermost ones about half the size of the lower ones, not confluent, with a distinct terminal pinnule which may be the smallest or the size of one of the larger ones. Veins 3–5 to a segment, forked at the base, somewhat raised adaxially, especially towards their ends. *Sori* continuous along the outer margin, the receptacle clearly visible on the ventral side as a wrinkle; indusium rigid, ca. 0.5 mm wide, repand-erose, almost equalling the margin, bulging, but usually hardly reflexed at full maturity. Sporangia ca. 230 × 185 μ; annulus with 9–12 indurated cells; spores medium brown, ca. 32–40 μ, 32?

Distribution: Sandstone regions of the Guiana Highlands (map 7). In scrub and bogs in savannas, among boulders and in sand, usually in locally moist places, from ca. 300–1400 m.

COLOMBIA. VAUPÉS: Cerro Isibukuri, near summit, Schultes & Cabrera 15046 (US).
VENEZUELA. AMAZONAS: Summit of Mt. Duida, Tate 731 (NY, US); ibid., Steyermark 58247 (F, MO, NY, US).
BRITISH GUIANA: Hooroobea-savanna, Jenman 3739 (BM, K); Kaietuk-savanna, Tutin 682 (BM, K, U, US); savanna near Mt. Roraima, Appun s.n. (B, W); Kaieteur-savanna, Im Thurn s.n. (K); Maguire & Fanshawe 23160 (A, F, K, MO, NY, U, US); Sandwith 1283 (BM, K, NY, U); Jenman s.n. (NY); Jenman 1382 (K); Line 28, right bank of Essequibo R., Guppy 157 (BM); without loc., Schomburgk 253 in part (B, HOLOTYPE; Isotype in BM); id. 146 in part (G, K, W); Appun 93 (B); id. 804 (K); Glaziou 12351 (prob. an Appun-coll.) (B, BR, C, C. Chr. in BM, G, K, LE); Lobscheid s.n. (W); Jenman s.n. (NY, US).

The differences between this species and its closest relative, *L. meifolia*, have been discussed under that species. *L. pendula* has been incorrectly reported from the state of Rio de Janeiro by CHRIST (in Schwacke, l.c., see above, and in Bull. Herb. Boiss. II, 2:637, 1902) on the base of the Glaziou-specimen cited above, which was probably collected by Appun, but provided with an incorrect label by Glaziou when it was added to his herbarium. It has never again been found in south-eastern Brazil, and its occurrence there is most unlikely.

6. **Lindsaea** x **dissecta** Kramer, hybr. nov. **Fig. 43**

(*Lindsaea meifolia* (H.B.K.) Mett. ex Kuhn × *L. pendula* Klotzsch.)

Inter *L. meifoliam* et *L. pendulam* interjecta; lamina apice minus sensim redacta, pinnulis inferioribus semel vel bis furcatis, superioribus cuneatis, integris, pinnulis *L. pendulae* similibus; sporis obscuris, ut videtur, abortivis.

Typus: Ll. Williams 13934 from Yavita, Amazonas, Venezuela (US.)

Intermediate between the two preceding species. *Petioles* 6–26 cm long, as long as to twice as long as the lamina. *Lamina* bipinnate + pinnatifid or + bipinnatifid, or mostly subtripinnate + pinnatifid or + bipinnatifid, rhombic to broadly lanceolate, 5–20 cm long; primary pinnae 6–15 to a side, the lower ones 2–5 cm long, the upper ones little reduced (in some small leaves the lamina gradually narrowed from base to apex), more abruptly reduced at the apex than in *L. meifolia*, and more gradually than in *L. pendula*, which has none or at most two reduced upper pinnae. Lower pinnae, rarely also higher ones, with 1 or 2 pinnate deflexed secondary pinnae to a side, these rarely quite absent. Ultimate *pinnules* pendulous, 3–4.5 mm long, variously incised; in sterile leaves the larger pinnules are three times bifid, the depth of the incisions decreasing in the lobes of higher order, the lobes lanceolate, acute; otherwise the pinnules mostly bifid, the upper lobe often shallowly cleft again; upper segments of fertile leaves often obovate-cuneate, entire, except for the erose outer margin, resembling those of *L. pendula*. Sori of various width, depending on the degree of dissection of the pinnules;

indusium erose to subentire. Sporangia as in the parent species; spores dark, ± collapsed, with wrinkled wall, apparently not viable.

Distribution: Only known from the type-collection (map 7).

VENEZUELA. AMAZONAS: Yavita, in low, somewhat moist situations, Ll. Williams 13934 (US, HOLOTYPE; Isotypes in F, GH).

The exactly intermediate leaf-pattern points to the hybrid-origin of this form; the abortive spores may be taken as proof for this assumption. Moreover, both *L. pendula* and *L. meifolia* occur in the region where the hybrid has been found. Small leaves may be rather strongly dissected and are closer to those of *L. meifolia*. This is the first hybrid in the genus described from the Western Hemisphere.

Sectio III. **Temnolindsaea** Kramer, sect. nov.

Lamina bipinnata, cum pinna terminali lateralibus conformi, raro simpliciter pinnata, pinnulis dimidiatis, plus minusve incisis, superioribus sensim redactis, soris interruptis.

Species typica: *Lindsaea klotzschiana* Moritz in Ettingshausen.

In this section the species with ± incised pinnules and interrupted sori are united. The lamina is mostly bipinnate *cum impari*, rarely simply pinnate, but never throughout a species. The upper pinnules are always gradually reduced.

7. **Lindsaea klotzschiana** Moritz in Ettingshausen, Farnkr. 212; t. 145 f, 1,2 (1865); Bot. Zeit. 12 (Beil.):855 (1854), *nomen*.

Type: Moritz 238 from Tovar, Venezuela (B!).

Heterotypic synonyms: *L. elegans* Fée, Gen. Fil. 106 (1852); Kuhn, Chaetopt. 26 (1882); non Hooker (1837). Type: Moritz 238 from Tovar, Venezuela (P!).

Homotypic synonym: *L. Feei* C. Christensen, Ind. Fil. 393 (1906); Hieronymus, Hedwigia 62:16 (1920); Knuth, Fedde Rep. Beih. 43 (1):31 (1926).

L. trapeziformis Dryand. var. *γ laxa* Baker, Fl. Bras. I^2:355 (1870), as to synon. and fig. (pl. 22 fig. 1), not as to specimen cited. Type: Moritz s.n., prob. 238, from Venezuela (K!).

Misapplied names: *L. guianensis* auct. non Dryand.; Knuth, Fedde Rep. Beih. 43 (1):31 (1926), in part.

L. quadrangularis auct. non Raddi; Knuth, l.c.

L. crenata auct. non Klotzsch.; A. C. Smith in Gleason & Killip, Brittonia 3:145 (1939).

Petioles brown to blackish, abaxially at least above angular; lamina bipinnate with conform terminal pinna, herbaceous or subcoriaceous; pinnules dimidiate-ovate to subtriangular, 1½—slightly over 2 × as long as wide, upper and outer margin incised; sori interrupted, mostly three per pinnule; spores trilete.

Rhizome creeping, prob. rather long, 1½–2½ mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2.8 mm long, 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close or rather close, (5–)10–52 cm long, mostly roughly as long as the lamina, ¾–2, mostly 1 mm in diam. near the apex, dull to shining, adaxially sulcate in the upper part, flattened or subterete below, or sulcate almost to base, abaxially subterete or at base only, the upper part flattened-angular or sulcate above, rarely angular almost to base. *Lamina* bipinnate, very rarely simply pinnate or subtripinnate, ca. 15–45 cm long, dark green on the ventral, paler on the dorsal side, with 1–8, mostly 2–5 primary pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole; axillary cushions very indistinct or obsolete. *Pinnae* rather strongly ascending, angle 20–40°, but often decurved in their upper part, the lower ones subopposite, the upper ones alternate, the lower 3–8 cm apart, 10–15(7–25) cm long, the upper ones closer, two-thirds to half as long, 1.5–2.5 cm wide, the terminal often widest, up to 3 cm, subsessile or with a stalk of 2–3 mm, in the terminal up to 2 cm, widest in the lower third or in the middle, slightly narrowed at the base, especially on the acroscopic side, very gradually narrowed above. Secondary rachises stramineous to reddish brown, adaxially with a deep constricted channel, abaxially subterete at the base, becoming suddenly angular at the level of the second or third pinnule, the upper part mostly sulcate. *Pinnules* ca. 10–30(–40) to a side, mostly alternate throughout, laxly ascending or the lower ones spreading, rarely slightly deflexed, subsessile, more than their width apart, the basal ones often considerably more, sometimes contiguous or even slightly imbricate, 8–14 mm long, 4.5–8 mm wide, a few basal pinnules somewhat reduced, a strongly reduced slightly decurrent axillary pinnule almost invariably present. Inner margin ± straight, mostly parallel to the sec. rachis, upper base shortly rounded, lower base shortly cuneate, hardly stalk-like, lower margin straight or slightly concave at the base, increasingly convex towards the apex, outer margin rounded or sometimes almost truncate, upper/outer margin more or less incised, in addition often minutely erose, in sterile pinnules (rarely found) with incisions ca. 1–1.5 mm deep, the teeth obtuse or acute. Marginal strand stramineous to pale brown, distinct but not conspicuous. Veins immersed or slightly raised abaxially, mostly once forked, their ends ¾–1 mm apart. Main vein hardly united with the marginal strand, ca. 0.4 mm above it near the apex. Upper pinnules very gradually reduced, a few denticuliform upper ones confluent with a linear blunt terminal segment 0.5–1.5 cm long, lobed below, crenate above, sometimes soriferous in the basal lobes. *Sori:* indusium pale, ca. 0.5 mm wide, not reaching the margin by ca. 0.2 mm, less often equalling it, ± reflexed and conceiled at full maturity. Sporangia 147–160 × 115–125 μ; annulus with 10–12 indurated cells; spores pale brown, ca. 26–28 μ, 32?.

Distribution: North-eastern and coastal Andes of Colombia and Venezuela, mountains of Venezuelan Guayana; scattered in Central America (map 9). In moist mountain-forests, from ca. 1000–2200 m, occasionally on trunks of trees; apparently not rare.

Vern.names: mantsána šižé (Colombia, Pittier); sumi-peu (Bolívar, Venezuela, Steyermark).

a. forma **klotzschiana**. **Fig. 45**

Pinnules herbaceous or, esp. in specimens from southern Venezuela, subcoriaceous, the incisions of the upper margin mostly 0.5, up to 1 mm deep; sori not in one line, at slightly different levels and forming small angles with each other, the basal and apical quadrinerval, the middle one binerval, or most of them binerval, occasional quadri-, qui- or sexinerval ones present; indusium subentire to erose or superficially lacerate.

GUATEMALA. ALTA VERAPAZ: Rubelpec, Finca Seamay, Wilson 187 (F).
COSTA RICA: Santiago–Picacho Mondongo, Brenez 16962 (F; very slender).
COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, Las Nubes, H. H. Smith 937 (BM, F, G, GH, K, L, MO, NY, PH, S, S-PA, U, US); ibid., hacienda Cincinnati, Martin 3324 (IA, MO, US); Dos Aguas, Carriker 26 (US); near S. Andrés de la Sierra, w. slope of the Cordillera, Pittier 1640 (GH, US).
Dept.?: S. Cristobal, Engel s.n. (LE).
Without exact loc., Karsten II (B).

VENEZUELA. MÉRIDA: near Tovar, Moritz 238 (B, HOLOTYPE; 7 Isotypes; BM, C, FI, G, GH, GOET, K, HOLOTYPE of *L. trapeziformis* var. *laxa*, and Isotype; L, LE; P, HOLOTYPE of *L. elegans* Fée and *L. feei;* S–PA, UPS); ibid., id. 164 (BR, C, C. Chr. in BM, NY); ibid., Fendler 63α, β (BR, G, GH, GOET, K, MO, PH, US); Mérida, Engel 208 (B).

CARABOBO: Hacienda Marture between La Entrada and Las Trincheras, Ll. Williams 11038 (F).

D.F.: Caracas, Linden 82 (G); Los Venados near Caracas, Allart 107 (NY, US); Cordillera del Avila, los Venados–Papelón, Steyermark 55094 (US).

MIRANDA: Between Antímano and Aguas Negras, Pittier 6019 (B, US).

BOLÍVAR: Cerro Apacará, Cardona 1530 (US); Cerro Guaiquinima, Upper R. Paragua, Cardona 969 (US); Ptari-tepuí, Steyermark 59739 (F, K, MO, NY, US); ibid., id. 59503 (F, MO, NY, US); Auyan-tepuí, Tate 1247 (NY, US); ibid., id. 1246 (NY).

State?: Cadena de la Silla, Vogl 667 (F, M).

Without exact loc.: Birschell s.n. (BM); van Lansberge 19 (L).

b. forma **sublacera** Kramer, f. nov. **Fig. 44**

Differt a forma typica incisionibus pinnularum valde irregularibus, altioribus, nonnullis usque ad 1 vel 2 mm altis, lobo apicali saepe prominente, soris fere omnibus binerviis, indusio margineque fertili magis erosis.

Typus: Haught 3831, east of Codazzi, Magdalena, Colombia (US).

Pinnules herbaceous; sori more pronouncedly on different levels and at larger angles with one another.

COLOMBIA. MAGDALENA: Forest 12 km east of Codazzi, Haught 3831 (US, HOLOTYPE; Isotypes in BM, GH, US); "Cincinnati", lower slopes of Mt. San Lorenzo, near Santa Marta, Seifriz 37 (GH, US; less typical).

SANTANDER: Las Cruces, Kalbreyer 933 (B, K).

L. klotzschiana is closest to *L. cultriformis*, where the differences are mentioned, also allied to *L. tetraptera*.

Comment on the synonymy: The name *Lindsaea klotzschiana* was published without a description and has been rejected for this reason. However, Ettingshausen's figure is quite good, showing essential characters, and leaves no doubt as to the identity of the depicted species. Therefore, Art. 43 of the Code of Nomenclature applies. CHRISTENSEN (1906, p. 394) referred it incorrectly to *L. lancea;* as the oldest name for the present species, *L. elegans* Fée, is a later homonym of *L. elegans* Hooker, he created a new name for it, *L. feei*, which is superfluous if *L. klotzschiana* is accepted as validly published. The name *L. laxa* Kunze ex Baker, listed by CHRISTENSEN (l. c., p. 394), was never validly published; it appears as *L. trapeziformis* var. β, *L. laxa* Kunze in *Synopsis Filicum*, p. 107, which is contrary to Art. 24 of the Code. It was, however, validly published in the rank of variety in Fl. Bras. I^2: 355, and in this connexion the question of typification arises. The only specimen cited is Spruce 2277 from Brazil (included in *L. tetraptera* in the present study), but this was not definitly designated as type, and in the author's opinion it should not be regarded as such. The synonyms cited by Baker and his figure all apply to *L. klotzschiana*, and two specimens in K bear Baker's name var. *laxa* in his handwriting; *L. klotzschiana* is cited as synonym with the invalid publication of "β, *L. laxa* Kunze", and both should therefore be based in the same type, Moritz 238 from Venezuela, which was, of course, not cited in Flora Brasiliensis as it is from outside Brazil. Even if this argumentation is not accepted, *L. tetraptera* has priority on the species-level, as *L. laxa* was never validly published in that rank.

8. **Lindsaea cultriformis** Kramer, spec. nov. **Fig. 37**

Misapplied names: *L. trapeziformis* auct. non Dryand.; Wright, Trans. Linn. Soc. Bot. II, 6:80 (1901). *L. crenata* auct. non Klotzsch; A.C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931).

Folia bipinnata; petiolo stramineo vel fuscescente, facie abaxiali tereti; lamina herbacea, laetevirens; pinnulis lanceolatis leviter falcato-decurvatis vel patentibus, latitudine circa partem tertium longitudinis aequante, margine superiore incisa, incisionibus plerumque minus quam 1 mm altis, pinnulis superioribus sensim redactis; soris interruptis, fere in venis duabus insidentibus, 4–6 in quaque pinnula; sporis tetraedriformibus.

Typus: Tate 893 from Mt. Duida, Amazonas, Venezuela (NY).

Rhizome creeping to obliquely ascending, about 3 mm in diam.; scales minute, ovate-lanceolate, acute to shortly acuminate, up to 0.6 mm long and 0.2 mm wide, with up to 7 rows of cells at the base. *Petioles* close, subdistichous, castaneous to atropurpureous at the base, about as long as the lamina, ½–1 mm in diam. near the apex, adaxially channelled. *Lamina* 20–35 cm long, with 3–4 pinnae to a side and a similar terminal one. *Primary rachis* similar to the upper part of the petiole, but the abaxial side in the upper half with a suddenly appearing groove. Axillary cushions conspicuous, dark. *Pinnae* subopposite or alternate, short-stalked (up to 1 cm) to sessile, 2½–5 cm apart, laxly ascending under an angle of about 45°, 8–20 cm long, the upper ones slightly shortened, 2–3 cm wide, slightly narrowed at the base, gradually narrowed above. Secondary rachises abaxially terete at the extreme base, above sulcate, the groove mostly suddenly appearing at the level of about the second pinnule, flattened towards the apex, adaxially with a deep narrow groove with almost touching borders. *Pinnules* 20–40 to a side, subopposite, the upper ones alternate, mostly about 14 mm long and 4–5 mm wide, the basal ones slightly shortened, a strongly reduced axillary pinnule sometimes present. Inner margin straight and more or less parallel to the sec. rachis, lower base hardly stalk-like, upper base rectangular or shortly rounded, upper margin increasingly convex towards the acute or subacute apex, no outer margin developed; lower margin approximately straight or mostly shallowly concave at the base, convex at the apex. Upper margin with shallow incisions, mostly 3–5 per pinnule, these deeper and wider in sterile pinnules. Marginal thickening pale brown, inconspicuous, except at lower base. Veins immersed but readily visible, once or the basal twice forked, ca. 1 mm apart at the margin; main vein hardly united with the marginal strand. Upper pinnules very gradually reduced, the uppermost ones denticuliform, confluent into a lobed or toothed, often caudate, up to 2 cm long apex. *Sori* mostly binerval, or the basal tri- or quadrinerval (rarely occupying up to 6 veins); indusium ca. 0.2 mm wide, firm, entire, fixed at the base and the greater part of the sides, equalling the margin, hardly or not reflexed at full maturity. The receptacle and the indusium laterally surpass the ends of the outer veins bearing the sorus. Sporangia ca. 142–150 × 100 μ; annulus with 9–12 indurated cells; spores hyaline, almost colourless, ca. 22–27 μ.

Distribution: North-western South America (map 8). In forests, from ca. 120–2000 m.

COLOMBIA. ANTIOQUIA: Amalfi, La Vivora, Kalbreyer 1650 in part (B, K); ibid., Lehmann XXXIII (BM, G, K, LE, US).
VENEZUELA. AMAZONAS: Mt. Duida, Tate 893 (NY, HOLOTYPE); Capihuara, Upper Casiquiare, Ll. Williams 15536 in part (GH).
BRITISH GUIANA: Mt. Roraima, McConnell & Quelch 617 (K, NY); without loc., Appun s.n. (herb. Glaziou 12357) (B, C, LE, NY).

Most closely allied to *L. klotzschiana*, probably also to *L. stenomeris*. In general aspect not unlike *L. decomposita* from the Old World. It is strange that this rather distinctive species, known from a number of collections the first of which of considerable age, has never been recognized.

9. **Lindsaea stenomeris** Kramer, spec. nov. **Fig. 46**

Folia pinnata vel bipinnata, petiolo badio, nitidulo, facie abaxiali inferne obtuse angulata subteretive, superne applanata, angulis pallidis; lamina membranacea; pinnulis laciniatis, laciniis obliquis, linearibus vel sublinearibus, nonnullis furcatis; pinnulis superioiribus sensim redactis; soris uninerviis; sporis tetraedriformibus.

Typus: Maguire, Wurdack & Bunting 37365 from Cerro de la Neblina, Amazonas, Venezuela (US).

Rhizome creeping, ca. 1.5–2 mm in diam.; scales lanceolate, acuminate, up to 0.65 mm long, 0.15 mm wide, with up to 5 rows of cells at the base. *Petioles* close, ca. 5–15 cm long, ⅓–¾ the length of the lamina, ¾–1 mm in diam. at the apex, abaxially bordered by pale ridges which gradually evanesce downwards, obsolete near the middle, the lower part obtusely angular to subterete, adaxially above similar to the abaxial side, but the stramineous borders extending farther downwards, gradually disappearing towards the terete or subterete base. *Lamina* dull dark green, narrowly lanceolate to linear when simply pinnate, ca. 10–20 cm long, when bipinnate with one or two pinnae to a side and a similar terminal one which resemble simply pinnate blades. *Primary rachis* similar to the upper part of the petiole, axillary cushions visible as distinct swellings. Simply pinnate laminae and primary pinnae 2½–3 cm wide, the latter patent under an angle of ca. 50°. *Pinnules* ca. 15–30 to a side, laxly ascending, alternate or the lower ones subopposite, rather close, the upper ones subcontiguous, short-stalked to subsessile, the largest 1½–2 cm long, 4–6 mm wide, approx. lanceolate in outline, ca. 3½–4 × as long as wide, the lower ones not or hardly reduced; a strongly reduced axillary pinnule present. Lower margin straight or faintly concave at the base, more strongly concave towards the apex, inner margin approx. straight, parallel or divergent, blade of the pinnule from the upper margin dissected by deep incisions, the divisions linear or slightly cuneate, obtuse, ca. 4–6 mm long, ¾–1 mm wide, connected by a narrow wing (0.1–0.3 mm), oblique, somewhat divergent, about 5 per pinnule, the largest mostly once forked, otherwise entire; base of pinnules cuneate, with a stalk-like base up to 1 mm long in which the dark colour of the rachis ends rather abruptly. Marginal strand stramineous, present throughout but weak except at the lower base. Main vein marginal at the base only, otherwise at the basiscopic side with a laminal wing ca. 0.2 mm wide. Veins immersed but evident, single in each lobe, in forked ones dichotomous considerably below the bifurcation. Upper pinnules rather suddenly shortened near the pinna-apex, of simpler structure, a few rather abruptly confluent into a pinnatifid apex. *Sori* uninerval (very rarely binerval); indusium usually semi-elliptic, attached at the base only, entire, ca. 0.4 mm wide, its edge 0.2–0.4 mm from the margin, not reflexed at full maturity. Sporangia protruding, 160–165 × 130 μ; annulus with 10–12 indurated cells; spores rather pale brown, 24–27 μ, 32?

Distribution: Only known from type-collection.

VENEZUELA. AMAZONAS: Cerro de la Neblina, Río Yatua; occasional on rocks in forest, 900 m, Maguire, Wurdack & Bunting 37365 (US, HOLOTYPE).

A second dubious specimen may represent a special form or subspecies; it has a simply pinnate lamina with much less incised pinnules with broader lobes, approaching those of *L. cultriformis*, but with many uninerval sori, and in other characters agreeing with *L. stenomeris:*

Venezuela. Bolívar: Chimantá-Massif, Toronto-tepuí, in *Clusia*-forest on slopes of Río Tirica below Summit camp, 1760–1880 m, Steyermark & Wurdack 1205 (US).

L. stenomeris is a very remarkable species as it is the only American representative with a type of leaf much more common in the Eastern Hemisphere, with strongly dissected, yet quite dimidiate pinnules (see also p. 126). Its closest relative is probably *L. cultriformis*, which, however, is rather different in freely bipinnate blades with pale axes, much less incised pinnules, and mostly binerval sori. It is at present impossible to say whether the strong dissection of the pinnules is a primitive character or whether it may be of secondary development, being derived from a type comparable to that of *L. cultriformis* or *L. klotzschiana*. It is to be hoped that new collections of this interesting species will show more of its range of variation and distribution.

10. **Lindsaea tetraptera** Kramer, spec. nov. **Fig. 38**

L. trapeziformis Dryand. var. *γ laxa* Baker, Fl. Bras. I²:355 (1870), as to specimen cited.

Folia pinnata vel vulgo bipinnata, petiolo badio, lucido, superne alis pallidis marginalibus quattuor instructo; lamina olivaceo-pulla vel nigricans, herbacea, rhachidibus secundariis quadrialatis; pinnulis leviter falcato-decurvatis, margine superiore incisa, incisionibus plerumque duabus vel tribus in quaque pinnula, vix ultra 0.8 mm altis; soris venas 2–4 vel ultra occupantibus; sporis tetraedriformibus.

Typus: Schultes & Cabrera 16503 from Cerro de la Gente Chiquita, Río Miritiparaná, Amazonas, Colombia (US).

Rhizome short-creeping, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.75 mm long, 0.25 mm wide, with up to 9 rows of cells at the base. *Petioles* close, about as long as the lamina or shorter (often incompletely collected), diam. 1–2 mm near the apex, castaneous, shining, subterete at the very base, adaxially below with small lateral ridges which soon pass into stramineous wings, abaxially similar wings present in the upper part which do not extend so far downwards, sometimes only to the middle; upper part of the petiole therefore four-winged, the surfaces between the wings somewhat convex. *Lamina* ca. 15–30 cm long, with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, but abaxially often channelled, especially at the base. Axillary cushions distinct, often darker. *Pinnae* mostly subopposite, laxly spreading under an angle of ca. 45–60°, subsessile or short-stalked (up to 5 mm), the terminal often with a longer stalk, 4–7 cm apart, ca. 12–25 cm long, 2–3½ cm wide, widest in the lower third, thence gradually but not strongly narrowed to the apex, slightly narrowed at the base, the upper ones somewhat shortened, the terminal about the size of the basal ones. Secondary rachises dark, with conspicuous spreading wings on the four edges which evanesce in the apical part, those of the adaxial side continuous with the wings of the primary rachis, those of the abaxial side either approaching each other below the lowermost pinnule and evanescing abruptly or sometimes merging into one which may be connected with the abaxial wing on the corresponding side of the primary rachis. *Pinnules* ca. 20–30 to a side, subopposite or mostly alternate, spreading or slightly deflexed, subsessile, separated by spaces equal to about half their width, (9–)12–18 mm long, (4–)5–7 mm wide, 2–2½ × as long as wide, broadest at the base, gradually narrowed to the apex, approximately dimidiate-ovate, ± falcate. Inner margin straight, ± parallel to the secondary rachis, lower base cuneate, hardly stalk-like, upper base shortly rounded, lower margin usually rather strongly concave, upper margin rather evenly convex, incised, with mostly 2 or 3 incisions 0.2–0.8 mm deep, narrow, with acute sinus, the margins otherwise entire; no separate outer margin developed the lower and upper edge meeting at the acute to obtuse apex which may bear a few sterile teeth in incompletely fertile pinnules. Upper edge of sterile pinnules with small crenulations in the basal part which become much larger towards the apex, the teeth obtuse, often more highly connected in pairs. Veins immersed but clearly visible, once or twice forked, their ends rather irregularly spaced, ca. ½–1 mm apart. Main vein not united with the marginal strand, ca. ⅓ mm above it near the apex. Marginal strand present throughout but inconspicuous except at the base of the lower margin. Upper pinnules gradually but not strongly reduced except just below the apex of the pinnae where a few 2–5 mm in length are present (rarely more gradually shortened), one or two connected by a wing with the terminal segment which is lanceolate, lobed at the base, otherwise serrate or crenate, 6–18 mm long, sterile or with small sori in the lobes, lanceolate. *Sori* along the upper/outer margin, interrupted, occupying 2–4 veins, the basal ones sometimes more, mostly 3–4 per pinnule. Indusium greyish, entire, ca. 0.2 mm wide, not reaching the margin by about the same distance, largely reflexed and conceiled at full maturity. Sporangia ca. 150 × 140 μ; annulus with 10–13 indurated cells; spores pale brown, ca. 23–25 μ.

Distribution: North-western South America (map 10). In forests and scrub, occasionally epiphytic, at lower altitudes, ca. 100–500 m.

COLOMBIA. AMAZONAS: Río Miritiparaná, Cerro de la Gente Chiquita, headwaters of Quebrada Guacayá, epiphytic, Schultes & Cabrera 16503 (US, HOLOTYPE).

VENEZUELA. BOLÍVAR: Cerro Guaiquinima, Upper Río Paragua, Cardona 899 (F, US).

AMAZONAS: Maroa, R. Guainía, Ll. Williams 14200 (F, US), 14264 (F, US); Capihuara, Upper Casiquiare, Ll. Williams 15533 (US).

BRITISH GUIANA: Potaro R., Jenman s.n. (NY); Rockstone, Essequibo R., Jenman s.n. (NY); without loc., Jenman s.n. (NY, US); Appun s.n. (Glaziou 12355 in part) (B, G, LE, NY, US).

BRAZIL. AMAZONAS: Near São Gabriel da Cachoeiras, Rio Negro, Spruce 2277 (B, BM, BR, G, K, W).

A very clear-cut and distinctive species, characterized by dark four-winged axes and interrupted sori. The closest relative seems to be *L. klotzschiana*. The author's views on the typification of *Lindsaea trapeziformis* Dryand. var. *laxa* Baker are explained under *L. klotzschiana*.

11. **Lindsaea parkeri** (Hooker) Kuhn, Chaetopt. 26 (1882); Posthumus, Fl. Surin. Suppl. 71 (1928); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Basionym: *Davallia Parkeri* Hooker, Spec. Fil. I: 176 (1844), t. 53 C; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 93; Baker, Fl. Bras. I^2:344 (1870), pl. 41 fig. 1; Jenman, W. Ind. Gui. F. 67 (1899).

Type: Parker s.n. from British Guiana (K!)

Homotypic synonym: *Odontoloma parkeri* (Hooker) Presl, Epimel. Bot. 97 (1849); Fée, Gen. Fil. 329 (1852); J. Smith, Hist. Fil. 269 (1875).

Petioles dark brown to atropurpureous, quadrangular; lamina simply pinnate or bipinnate with conform terminal pinna, thinly herbaceous; pinnules ovate to triangular or subtrapeziform, 2–2½ ×

as long as wide, shallowly incised to subentire; sori interrupted, uninerval or the outer ones bi—quadrinerval; spores trilete.

Rhizome rather short-creeping, ¾–1 mm in diam.; scales lanceolate, acuminate, up to 1 mm long and 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* rather close, from less than 1 to 16 cm long, much shorter than the lamina in small leaves, slightly longer in large ones, diam. 0.3–1 mm at base of lamina, often shining, quadrangular or terete at the extreme base, the surfaces more or less flat, with sharp, above often paler angles. *Lamina* from about 3 cm in apparently depauperate specimens to about 15 cm long, blackish-green on the ventral, paler on the dorsal side. *Rachis* similar to the stipe, but often paler, and the paler colour of the angles often more distinct, the abaxial and adaxial surfaces concave. *Pinnules* not very close, not contiguous, the basal ones farther apart, about 15–35, mostly 18–20 to a side, the lower ones subopposite, the upper ones usually alternate, subsessile, gradually reduced above, finally confluent into a short, lanceolate, serrate-lobed, subacute terminal segment. Lower margin of pinnules straight or convex, or concave in large leaves, inner margin straight, mostly somewhat divergent, upper edge crenulate or lobed, convex, a separate outer margin hardly developed, apex rounded. Marginal strand hardly developed. Veins immersed, simple or the basal ones once forked, lax, 1–2 mm apart at the margin; main vein departing from the marginal strand near the base, rather divergent from the lower margin and up to 1 mm above it near the apex. *Sori* more or less interrupted; indusium delicate, ca. 0.4–0.6 mm wide, the upper edge erose-denticulate. Sporangia ca. 180 × 140 μ, annulus with 11–15 indurated cells; spores medium brown, ca. 28–32 μ, 32?.

Key to the subspecies:

1. a. All or the great majority of the sori uninerval; upper edge of pinnules mostly lobed; lamina pinnate or bipinnate . . . . . a. ssp. *parkeri*
   b. At least the outer sori bi—quadrinerval; upper edge of pinnules crenate or erose; simply pinnate . . b. ssp. *steyermarkiana*

a. ssp. **parkeri**. **Fig. 40**

Lamina pinnate or less often bipinnate, 10–20, mostly about 14 mm wide and acuminate when once pinnate, with 1–3 primary pinnae to a side and a conform terminal pinna when bipinnate; pinnae 5–12 cm long (the terminal one largest), subsessile, with a reduced axillary pinnule, otherwise similar to once pinnate laminae. Pinnules 5–10 mm long, 2.5–5 mm wide, mostly 2 (up to 2½) × as long as wide, the lower ones spreading, the upper ones ascending, in large leaves the basal ones occasionally somewhat decurved; upper edge lobed with incisions up to ¾ mm deep or sometimes sinuous only, in addition erose-crenulate; in sterile pinnules lobed, not erose. Sori uninerval, rarely binerval, 3-6 per pinnule; indusium semi-elliptic to semi-orbicular or subreniform, attached by its straight or slightly concave base only, not reaching the margin by about its own width, reflexed at full maturity.

Distribution: Guayana; on moist rocks, often along watercourses, sometimes periodically flooded, from 525 to ca. 1000 m. Apparently uncommon (map 11).

Venezuela: Bolívar: Chimantá-Massif, Abácapa-tepuí, Steyermark 74809 (US). British Guiana: Wismar, Demerara R., Jenman s.n. (NY); Macouria Creek, Essequibo R., Jenman s.n. (NY), Jenman 2284 (BM, K), Fanshawe M 329 (BM, K); Moraballi Creek, Essequibo R., Persaud 18 (K); Arrowye Creek, Essequibo R., Lobscheid s.n. (W); Essequibo R., without exact loc., Appun s.n. (K, W), Appun 30 (B); Amaku, Potaro R., Im Thurn s.n. (K); Sheenabowa, Potaro R., Jenman 1379 (K); Potaro R., above Kaieteur Falls, Sandwith 1391 (BM, K, U); Potaro R. Gorge, Amatuk Portage, Maguire & Fanshawe 23543 (NY, US); Kaieteur Savannas, Maguire & Fanshawe 23413 (K, NY, US);

Demerara and Potaro Rs., Jenman s.n. (NY); without exact loc., C. S. Parker s.n. (K, HOLOTYPE).
SURINAME: Tafelberg, Lower Augustus Creek, Maguire 24731 (A, F, K, NY, U, US).

b. **ssp. steyermarkiana** Kramer, ssp. nov.

Recedit a ssp. typica foliis semper simpliciter pinnatis, pinnulis margine superiore minus lobatis, soris, praecipue exterioribus, bi-quadrinerviis.

Typus: Steyermark 60229 from Bolívar, Venezuela (US).

Resembling in most respects simply pinnate forms of ssp. *parkeri*, but pinnules much less lobed, often hardly at all; sori, especially the outer ones, occupying 2–4 veins, but uninerval ones mostly present besides; indusia firmer, almost reaching the margin.

Distribution (map 11):

VENEZUELA. BOLÍVAR: Salto de Iwaracarú-merú at western end of Sororopán-tepuí, alt. 1615 m, Steyermark 60229 (US, HOLOTYPE; Isotypes in F, MO, NY); Ptari-tepuí, forested slopes along Large Lunch River below Misia Kathy Camp, alt. 1500 m, Steyermark 59454 (F, NY, US, Paratypes).

L. parkeri is easily recognized by the dark axes and small pinnules and particularly by the interrupted sori but hardly incised upper margin. The latter character is not observed in any other neotropical species, but is found in such Old World-species as *L. macraeana*. Its affinity is not clear; it is placed with misgivings in the present section.

Sectio IV. **Lindsaea**.

The bulk of the species belong to this section. The lamina is bipinnate (rarely subtripinnate or tripinnate), with a conform terminal pinna, or simply pinnate; pinnules dimidiate (rarely at the base only), with continuous or (in the largest pinnules) slightly interrupted sori; the upper pinnules are reduced or not.
Type species: the same as that of the subgenus.

Subsectio 1. **Subinterruptae** Kramer, subsect. nov.

Pinnulae maximae semel vel bis incisae, incisionibus soros interrumpentibus, minores integrae, soris continuis.
Species typica: *Lindsaea ovoidea* Fée.
Additional characters are dark petioles and trilete spores.

12. **Lindsaea ovoidea** Fée, Crypt. vasc. Brés. II:21 (1872/73). **Fig. 23, 39**

Type: Glaziou 4381 from Serra dos Orgãos, Rio de Janeiro, Brazil (P!).

Heterotypic synonym: *Lindsaea Christii* Rosenstock, Fedde Rep. 4:292 (1907). Type: Wacket s.n. from Serra do Mar, São Paulo, Brazil (M!).

Misapplied name: *L. trapeziformis* Dryand. var. *laxa* auct. non Kunze; Rosenstock, Hedwigia 43:216 (1904).

Petioles dark reddish brown to blackish, at least above sharply quadrangular; lamina bipinnate with conform terminal pinna, herbaceous to chartaceous; pinnules dimidiate-ovate, rhombic, or almost rectangular, ca. 2 × as long as wide, the smaller ones entire, the larger ones often with one incision in the upper and one in the outer margin, the upper ones gradually reduced; margins often slightly revolute; sori continuous or slightly interrupted; spores trilete.

Rhizome short-creeping, ca. 1 mm in diam.; scales lanceolate, long-acuminate, up to 2 mm long and 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close, 11–27 cm long, about as long as the lamina, ca. ¾ (½–1¼) mm in diam. near the apex, shining, below obtusely quadrangular apart from the subterete base, above sharply quadrangular, the adaxial side sulcate, the groove with paler margins, abaxially and laterally flattish or shallowly concave. *Lamina* bipinnate, very rarely simply pinnate, 12–25 cm long, ca. 9–17 cm wide, from as long as wide to almost twice as long, often somewhat spongiose, medium green on the ventral, slightly paler on the dorsal side, with 1–6 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, rarely paler. Axillary cushions not seen. *Pinnae* alternate or the lower ones subopposite, rather remote, the lower ones 2–5½ cm apart, the upper ones in plurijugate leaves about half as far, spreading at an angle of 40–50° (rarely more), 6–15 cm long, 1–2.5(–3) cm wide, not or hardly narrowed at the base, gradually narrowed in the upper half or two-thirds, subsessile, the terminal short-stalked; upper pinnae of plurijugate leaves about half as long as the lower. Secondary rachises adaxially sulcate, abaxially with a short basal terete portion, above, at the level of the first to third pinnule, with a rather abruptly appearing groove, which may sometimes be virtually absent in the upper pinnae of plurijugate leaves, mostly stramineous, the dark colour of the primary rachis ending rather suddenly in or just above the base of the pinna, rarely extending into it for a greater distance. *Pinnules* ca. 10–20 to a side, 8–17 mm long, 4–8 mm wide, widest at the base or of equal width almost throughout, almost invariably alternate, spreading or somewhat ascending, subsessile to short-stalked (up to 1.5 mm), a flabellate axillary pinnule mostly present, sometimes a few additional basal pinnules somewhat reduced. Lower margin straight or faintly concave, inner margin straight or somewhat convex and then often touching or overlying the secondary rachis, outer margin broadly rounded, rarely subtruncate, entire, or, especially in sterile pinnules, superficially crenate, upper margin irregularly and shallowly crenate in sterile pinnules, otherwise entire or often, esp. in larger pinnules, with one rather deep incision at $^3/_5$ of the distance to the apex, a similar incision not rarely found above the middle of the outer margin, thus the apex of the pinnule on a lobe which may be a little protracted. Marginal thickening very inconspicuous, except at the lower base. Veins immersed, obscure, once or twice forked, rather lax, ¾–1 mm apart at the margin; main vein somewhat elevated at the base, especially on the dorsal side, ca. ½ mm above the margin. Upper pinnules gradually reduced, the uppermost ca. 2.5–5 mm long, joined by a narrow wing, then rather suddenly confluent into an irregularly lobed, lanceolate-caudate terminal segment up to 1 cm long, obtuse or subacute, sometimes soriferous at the base. *Sori* continuous along the upper and outer margin, or, esp. in larger pinnules, often once or twice interrupted by the larger incisions. Indusium pale, greyish, ca. 0.4 mm wide, subentire or faintly erose, not reaching the margin by half its width to almost equalling it, ± reflexed at full maturity. Sporangia ca. $130 \times 115\ \mu$; annulus with 9–11 indurated cells; spores medium brown, ca. 23–28 μ, 16?

Distribution: South-eastern Brazil (map 12). Terrestrial in forests, from ca. 250–1200 m.

BRAZIL. MINAS GERAIS: Without loc., Damazio s.n. (RB).

RIO DE JANEIRO: Serra dos Orgãos, Glaziou 4381 *) (P, HOLOTYPE; Isotypes in B, C); id. s.n. (S-PA); near Rio, Glaziou 7957 (B, C, G, K, LE, M); without loc., Glaziou 7892 (B, C, K), 11701 (B, C, FI, K).

SÃO PAULO: Rio Grande, Serra do Mar, Wacket s.n. (Rosenstock-exs. 320) (M, HOLOTYPE of *L. Christii;* Isotypes in NY, S-PA, photogr. in BM); Serra do Itatins, Brade 8261 in part (S-PA, UC); ibid., id. 8260 (BM).

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*) On the label and with Fée's citation no. 3481 is given, but the tag attached to the plant and the duplicates bear no. 4381, which may be assumed to be correct.

Paraná: Volta Grande, Dusén 3730 (UC); Serra do Mar, Mt. Marumby, Dusén 3733 (BM, G).

Santa Catarina: Morro Queimados, Pelhoça, Spannagel 214 (NY, S–PA, UC); São Francisco, Stadtberg, Ule 144 (B, US); Joinville, Schmalz 133 (F, MO), 134 (NY); Pirai, Schmalz s.n. (F); Blumenau, Heins 13 in part (US); Pilões, Pelhoça, Reitz & Klein 2427 (HBR); Spitzkopf, id. 545 (BM); Brusque, Reitz C 1906 (S).

A clear-cut, yet not very distinctive species; the closest relative is *L. botrychioides* which may be derived from it; it is distinguished by almost always simply pinnate leaves and at the apex flabellate-widened lower pinnules. Smaller pinnules of both species are very similar, and the incisions of the margin in larger pinnules—one in the upper, one in the outer margin—are also a common feature.

Two sheets of Glaziou 7959 (B) from Brazil, probably from Rio de Janeiro, are intermediate between *L. ovoidea* and *L. virescens*. The leaves are bipinnate (one with one sec. pinna), the upper pinnae shortened, the basal pinnules of the terminal pinna large and subpinnate, the other pinnules more incised than in *L. ovoidea* and less than in *L. virescens*, but more like those of the former. They may represent a hybrid; the spores are, however, not abortive.

13. **Lindsaea botrychioides** St. Hilaire, Voy. Distr. Diam. 1:379 (1833); Kunze, Bot. Zeit. 8:328 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 105; Baker, Fl. Bras. I^{2}:352 (1870); Kuhn, Chaetopt. 26 (1882); Christ in Schwacke, Plant. Nov. Min. II:30 (1900); Diels, N. Pfl. I^{4}:221 (1902); Rosenstock, Hedwigia 46:79 (1906); Sampaio, Arch. Mus. Nac. Rio de Jan. 32 pl. 12 f. 6 (1930); Dutra, An. Prim. Reun. S. —Am. Bot. 2:29 (1938); not of Jenman, W. Ind. Gui. F. 75 (1899). **Fig. 47, 48**

Type: St. Hilaire 421$^{\text{bis}}$ from the Serra da Piedade, Minas Gerais, Brazil (P!).

Heterotypic synonym: *L. botrychioides* St. Hil. var. *subbipinnata* Rosenstock, Hedwigia 46:79 (1906). Type: Wacket 161 from Rio Grande, São Paulo, Brazil (S-PA!).

Petioles dark reddish brown to atropurpureous, quadrangular almost throughout; lamina simply pinnate, herbaceous to chartaceous; pinnules 1½–2 × as long as wide, the largest asymmetrically flabellate, widened in the outer part, often with two incisions as in the preceding species, smaller pinnules rounded-rectangular to subovate, entire; upper pinnules gradually reduced, the terminal free or almost free; sori continuous or slightly interrupted; spores trilete.

Rhizome short-creeping, 1–1.5 mm in diam.; scales lanceolate, acute-acuminate, very small, not over 0.5 mm long and 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* very close, ± distichous, (5–)10–24 cm long, usually about as long as the lamina, but sometimes not more than half as long, 0.6–1.2 mm in diam., rather shining, duller at the base, adaxially grooved, the groove rather deep and extending almost to the base, abaxially grooved in the upper part, the groove wide and shallow, becoming flat downwards with evanescing angles, subterete at the extreme base. Borders of the adaxial groove stramineous at least above, those of the abaxial groove sometimes paler above. *Lamina* simply pinnate (very rarely subbipinnate, with one or one pair of lower pinnae cleft or lobed or truly pinnate, with up to 10 pinnules to a side), approximately linear, (9–)14–34 cm long, 2–3½ cm wide, gradually narrowed in the upper half or mostly third to fourth, bright to dark green on the ventral, paler on the dorsal side. *Rachis* similar to the upper part of the petiole, upwards reddish; the abaxial groove narrowed above, its borders joining into a keel which evanesces in the base of the terminal segment. *Pinnules* ca. 15–25 to a side, alternate or the lower sometimes opposite, spreading, the basal wide-spaced, 1.5–4.5 cm apart, the upper ones gradually closer, but not or only the uppermost ones contiguous; largest pinnules with a short stalk up to 3 mm long, smaller ones subsessile; the largest 9–21 mm long, 6–14 mm wide, mostly widest in the outer third; shape rather variable: small pinnules are rounded-rectangular to subovate, large pinnules asymmetrically flabellate, often superficially lobed. Inner margin truncate, often slightly concave, the upper base acute or shortly rounded, sometimes touching or somewhat overlying the rachis, lower margin ± straight, in large pinnules concave, upper margin evenly rounded or almost straight in small pinnules, sinuous-convex in larger ones, usually with a concave portion or a shallow incision near the middle and one in the middle of the outer margin; the apex broadly rounded or almost truncate. Margin hardly thickened, sometimes crispate-undulate and/or minutely erose-repand in fertile pinnules, shallowly crenate, often with two deeper incisions as described above, in addition usually slightly revolute in sterile ones. Lower pinnules not reduced, or a few remote ones occasionally slightly smaller, upper pinnules gradually reduced, the apical ones 3–11 mm long; terminal segment asymmetrically lanceolate, very obtuse, 7–13 mm long, lobed on one or rarely on both sides of the base, mostly free, but sometimes connected by a very narrow wing with one or two upper pinnules, mostly fertile at the side, with a short abaxially keeled midrib. Veins twice or rarely three times forked, rather lax, their ends irregularly spaced at the margin, ca. ¾–1 mm apart, mostly immersed and rather obscure; main vein running ca. ½ mm above the lower margin. *Sori* along the upper/outer margin, continuous or in larger pinnules usually once or twice interrupted by the incisions of the margin; indusium greyish, ca. 0.5 mm wide, not reaching the margin by about the same distance, subentire or usually rather superficially erose-repand, commonly reflexed and conceiled at full maturity. Sporangia ca. 145 × 110–115 μ; annulus with 11–13 indurated cells; spores medium brown, ca. 25 μ, 32?

Distribution: South-eastern Brazil (map 13). Terrestrial in forests, often in moist places, up to 1650 m.

Representative specimens:

BRAZIL. MINAS GERAIS: Serra da Piedade, St. Hilaire 421bis (P, HOLOTYPE); Ouro Preto, Morro São Sebastião, Damazio s.n. (RB 36245).

RIO DE JANEIRO: near Rio, Glaziou 7958 (B, C, C. Chr. in BM, G, K).

SÃO PAULO: Alto da Serra, Estação Biologica, Gehrt 7830 (GH, NY); ibid., L. B. Smith 1904 (C, GH, US); Rio Grande, Wacket 161 (S–PA, HOLOTYPE of var. *subbipinnata* Ros.; Isotypes in NY, UC); Bosque da Saude, Brade 5174 (NY, UC); Serra da Bocaina, Brade 20644 (RB).

PARANÁ: Lucena, Wielewski 78 (Rosenstock-exs. 66) (B, BM, L, M, NY, RB, S, SI, S–PA, UC, US, W); Roça Nova, Dusén 8334 (B, BM, K, NY, S, S–PA, US); Jaguariaiva, Dusén 1411 in part (GH), 18036 (C. Chr. in BM, GH, MO, S–PA).

SANTA CATARINA: São Francisco, Schmalz s.n. (MO).

Reported from Rio Grande do Sul by DUTRA (1938).

The closest relative of this species is *L. ovoidea*, which agrees in dark axes, general shape of the smaller pinnules, revolute sterile margin, and incised larger pinnules with once or twice interrupted pinnules, but can be distinguished by more gradually confluent upper pinnules, never flabellately widened pinnules, and mostly bipinnate leaves. As the latter character is generally unreliable in the genus, the subbipinnate form of *L. botrychioides* described as a variety by Rosenstock does not deserve special recognition. *L. botrychioides* is not closely related to *L. flabellulata*, as was suggested by HOOKER &BAKER (1868, p. 105), nor to *L. guianensis* (id. 1874, p. 105). *L. crenulata* Fée and *L. multifrondulosa* Fée were incorrectly referred *L. botrychioides* in the first-cited publication.

Subsectio 2. **Decrescentes** Kramer, subsect. nov.

Pinnulae fertiles omnes integrae vel subintegrae, superioribus plus minusve decrescentibus, segmento terminali haud libero; soris continuis.

Species typica: *Lindsaea quadrangularis* Raddi.

14. **Lindsaea quadrangularis** Raddi, Opusc. sci. Bol. 3:294 (1819); Fl. Bras. Nov. Gen. Spec. I:55 (1825), t. 74; Hooker, Spec. Fil. I:214 (1844), in part; Ettingshausen, Farnkr. t. 146 fig. 1–3 (1865); Fée, Crypt. vasc. Brés. I:29 (1869), p.p. min.; J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928); not of Moore, Ind. Fil. I pl. 22 (1857); Mettenius, Ann. sci. nat. V, 2:217 (1864); Posthumus, Fl. Surin. Suppl. 75 (1928).

Type: Raddi s.n. from the vic. of Rio de Janeiro, Brazil (PI!). Homotypic synonym: *L. lancea* (L.) Bedd. var. *quadrangularis* (Raddi) Rosenstock, Hedwigia 46:80 (1906); Dutra, An. Prim. Reun. S.-Am. Bot. II:29 (1938).

Misapplied names: *L. trapeziformis* auct. non Dryander; Langsdorf & Fischer, Ic. Fil. p. 21, pl. 24 (1810); Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.; Rosenstock, Hedwigia 43:216 (1904), in part.

L. curvans of Fée, Crypt. vasc. Brés. I:29 (1869), in part, non Fée, 1852.

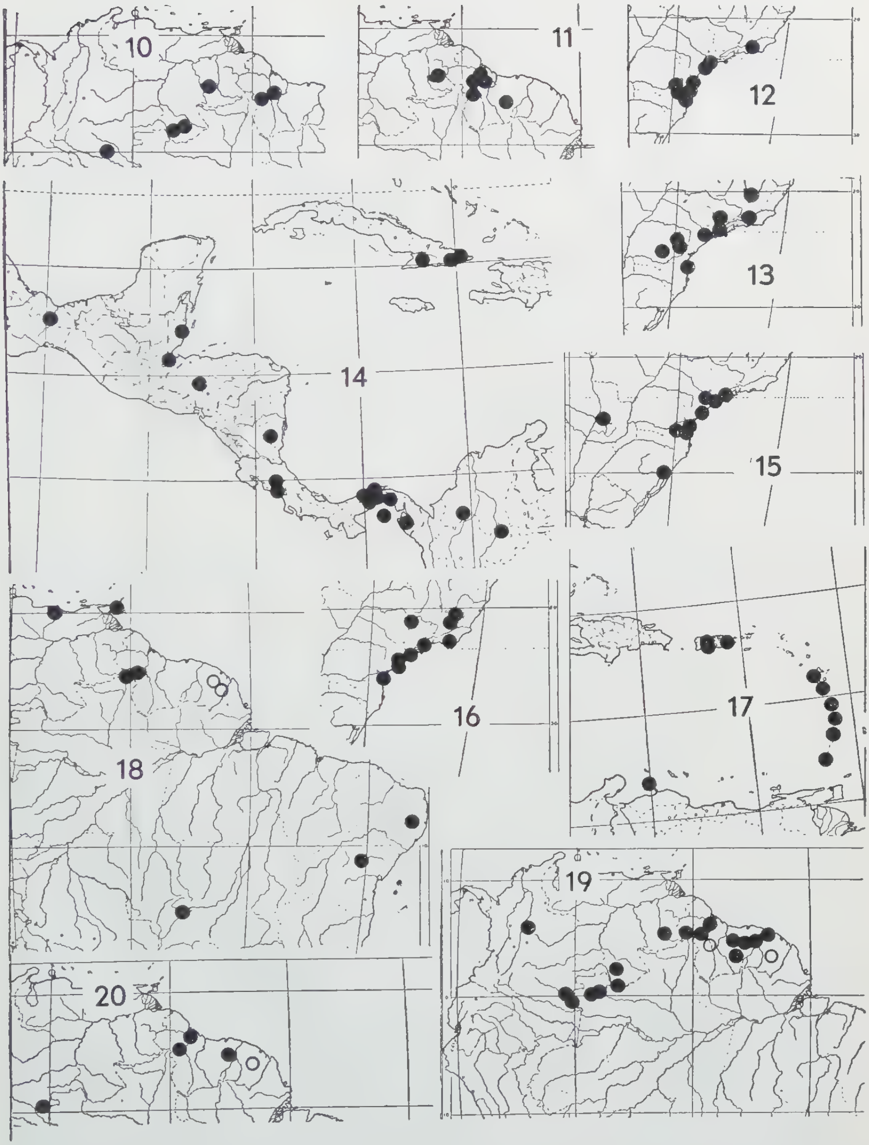
L. guianensis auct. non Dryander; Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.

L. lancea (L.) Bedd. f. *montana* (Fée) Lindman, Ark. f. Bot. I:198 (1903), as to specimens cited, not as to type.

Rhizome creeping, 1.5–3 mm in diam.; scales lanceolate, acuminate, up to 1.5–2 mm long and 0.3–0.4 mm wide, with up to 8 rows of cells at the base. *Petioles* rather close to close, ca. 10–60, mostly about 15–40 cm long, about as long as to twice as long as the lamina (less often only half as long). *Lamina* bipinnate (very rarely simply pinnate or subtripinnate), herbaceous, medium to dark green or olivaceous on the ventral, paler on the dorsal side, 15–40 (–50) cm long. *Pinnules* rather close but mostly not contiguous, usually dimidiate-ovate or -oblong, sometimes rhombic or trapeziform, 2–2½ × as long as wide, the upper ones ± reduced, ± confluent with the terminal segment. Veins immersed, once or twice (or three times) forked. *Sori* continuous along the upper/outer margin.

This species consists of four clear-cut subspecies which can be distinguished as follows:

1. a. Upper pinnules but little reduced, terminal segment large, almost free . . . . c. ssp. *terminalis*
b. Upper pinnules gradually and strongly reduced, confluent into a narrow, mostly small terminal segment 2



Map 10: *L. tetraptera.* Map 11: *L. parkeri;* complete dots: ssp. *parkeri;* half dot: ssp. *steyermarkiana.* Map 12: *L. ovoidea.* Map 13: *L. botrychioides.* Maps 14–17: *L. quadrangularis;* map 14: ssp. *subalata;* map 15: ssp. *terminalis;* map 16: ssp. *quadrangularis;* map 17: ssp. *antillensis.* Map 18: *L. pallida.* Map 19: *L. dubia.* Map 20: *L. surinamensis.*

2. a. Secondary rachises pale, abaxially with a groove starting abruptly above the subterete base . . . d. ssp. *antillensis*
   b. Secondary rachises with pale ± wing-like margins bordering a dark concave or flat central portion . . . a. ssp. *subalata*
   c. Secondary rachises mostly dark, terete at the base, gradually becoming angular, sulcate above, without wing-like margins 3
3. a. Spores monolete . . . . b. ssp. *quadrangularis*
   b. Spores trilete. . . . . . . atypical specimens of ssp. c.

a. ssp. **subalata** Kramer, ssp. nov. **Fig. 50**

Misapplied name: *L. horizontalis* auct. non Hooker; Standley & Record, Field Mus. Publ. 350:64 (1936).

Petiolus griseo- vel rubro-fuscus vel pullus, facie abaxiali plerumque angulari, raro subtereti; lamina bipinnata, pinnis patentibus, rhachidibus secundariis rubro-fuscis, facie abaxiali marginibus plus minusve aliformibus stramineis limbatis; pinnulis herbaceis, atrovirentibus vel olivaceis, superioribus sensim redactis; indusio pallido, angusto, 0.1–0.2 mm lato, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Skutch 2241 from the vicinity of El General, San José prov., Costa Rica (US).

Rhizome often strongly branched. *Petioles* 1–2 mm in diam. near the apex, ± shining, quadrangular except at the subterete base, less often (especially in Cuban specimens) the abaxial side terete, the surfaces, especially the adaxial one, often sulcate, the angles often more acute and paler in the upper part. *Lamina* with 1–7 pinnae to a side and a conform terminal one. *Primary rachis* reddish to dark brown, adaxially with a broad shallow groove with pale, not wing-like borders, abaxially terete, angular, or sulcate, in the latter case often with paler margins; transitions sometimes found in a single leaf. *Pinnae* alternate or the lower ones mostly subopposite, subsessile, the lower ones 3–5 cm apart, the upper ones little or not closer, laxly ascending under an angle of ca. 30–50°, the largest 12–25 cm long, 1¾–2½ cm wide, slightly narrowed at the base, gradually narrowed from slightly above the base to the apex, the upper ones mostly somewhat shortened. Terminal pinna usually longest and widest (up to 3 cm). Secondary rachises reddish-brown, adaxially with a narrow groove bordered by pale, not wing-like margins, abaxially with pale membranous wings sharply contrasting with the reddish flat or sulcate middle portion, ending rather abruptly at the level of approximately the second pinnule, the extreme base terete. *Pinnules* 20–30(–40) to a side, almost invariably alternate, spreading or slightly ascending, subsessile or shortly stalked (up to 0.5 mm), sometimes subfalcate or truncate-subtriangular, 8–16 mm long, 3.5–7 mm wide, a strongly reduced axillary pinnule present, 1–3 adjacent basal ones often ± reduced. Inner margin straight, parallel or slightly overlying the sec. rachis, lower base cuneate, ± stalk-like, upper base subangular, upper margin straight or sometimes faintly concave at the base, convex towards the apex, sometimes slightly crispate, lower margin straight or mostly faintly S-shaped, slightly concave at the base; apex rounded or subtruncate, in the latter case a distinct outer margin developed; pinnules widest at the base but not rarely hardly narrowed close to the apex. Marginal thickening whitish, inconspicuous except at the base of the lower margin; all margins entire or the upper minutely erose in fertile pinnules, sterile pinnules similar or sometimes with a ± prolonged apex, though never as pronouncedly as sometimes in *L. arcuata*, upper/outer margin shallowly crenate. Vein-ends ca. 1 mm apart, main vein hardly or not united with the marginal strand, but close to it, ca. ¼ mm above it near the apex. Upper pinnules gradually and strongly reduced, the highest 2–5 mm long, confluent with the terminal segment which is rather variable, asymmetrically-triangular or lanceolate, lobed at the base, ¾–1½ cm long, obtuse or subacute, or long-caudate, linear, up to 3 cm long, subacute, sterile or soriferous in the basal lobes. Indusium not reaching the margin by its own width to twice its width, rarely almost equalling it, ± reflexed at full maturity; sporangia ca. 145 × 115 μ; annulus with 11–13 indurated cells; spores ca. 25 μ.

Distribution: Cuba and southern Mexico to Colombia (map 14). In moist forests, sometimes along streams, from sea-level to ca. 1500 m.

Representative specimens:

CUBA. ORIENTE: Navas-Sierra de Buena Vista, Ekman 3856 (S, US); ibid., Shafer 4432 (GH, NY, US); Taco Bay between Rs. Santa Maria and Jiguaní, Ekman 3770 (K, NY, S, US); Río Yao, Marie-Victorin 21394 (GH, US).
MEXICO. VERA CRUZ: Coatzacoalcos, Ch. L. Smith 2078 in part (MO).
OAXACA: Without loc., Buchinger 343 (B).
BRITISH HONDURAS: Mullins River Road, Schipp 200 (B, BM, F, G, GH, K, NY, S, S–PA, UC, US).
GUATEMALA: Livingston, Deam 489 (GH).
HONDURAS: El Sauce, Santa Barbara prov., L. O. Williams & Molina 17692 (US).
NICARAGUA: Rama, Carhart s.n. (NY).
COSTA RICA: Vic. of El General, San José prov., Skutch 2241 (US, HOLOTYPE; Isotypes in K, MO, NY, S–PA); San Isidro del General, ibid., Scamman 5911 (GH); ibid., Chrysler & Roever 5216 (MO, UC); Finca los Cusingos near San Isidro del General, Norby & Norby 25 B, 370 (EAP); vic. of Pejivalle, Cartago prov., Standley & Valerio 47056 (US).
PANAMÁ: Chagres, isthmus, Fendler 412 (K, MO, US); Chico Trail, R. Indio, C.Z., Steyermark & Allen 17463 (G, K, MO, S, US); e. of Las Cascadas, C.Z., Maxon 4888 (GH, M, MO, NY, Pic.-Ser., S, US); San José Island, Perlas Archipelago, Johnston 477 (BM, GH, Pic.-Ser., S, U, US); Loma de la Gloria near Fató, Colón prov., Pittier 4080 (GH, NY, US); Cana-Cuapi-trail, Chepigana distr., Darien prov., Terry & Terry 1467a (F, US); Juan Diaz, Killip 2550 (B, S–PA, US).
COLOMBIA. BOLÍVAR: Boca Antizales, R. Esmeralda, Pennell 4473 (F, GH, K, MO, NY, US).
SANTANDER: Vic. of Barranca Bermeja, Magdalena Valley, Haught 1513 (GH), 1519 (F, GH, UC, US).

Usually ssp. *subalata* is easy to distinguish by the character of the secondary rachises, but it is sometimes difficult to separate it from *L. arcuata*, where the differences are discussed. From *L. portoricensis*, the only other species with which it is likely to be confused, it can be distinguished by more patent pinnae, continuous pale margins on the abaxial side of the sec. rachises, abaxially mostly angular petioles and narrower, entire indusia.

b. ssp. **quadrangularis.** **Fig. 51**

Petioles dark reddish brown to blackish, abaxially angular or subterete; secondary rachises stramineous to reddish brown, abaxially terete at the base, above gradually angular and/or sulcate; fertile pinnules subentire to erose-denticulate along the upper/outer margin, sterile ones crenate-dentate; upper pinnules gradually and strongly reduced, confluent; spores monolete.

Petioles 1–2 mm in diam. near the apex, dark reddish-brown to blackish, rather dull, subterete at the extreme base, otherwise quadrangular, with often sulcate surfaces, or the abaxial side obtusely angular to subterete. *Lamina* with 1–9(–11) pinnae to a side and a conform terminal one. *Primary rachis* reddish to dark brown, abaxially angular to subterete, sometimes sulcate above. *Pinnae* subopposite or alternate, short-stalked (a few mm) or mostly subsessile, the lower ones 2–6 cm apart, the upper ones closer, laxly ascending under an angle of 30–50°, the lower ones ca. 10–25 cm long, 1¾–3, mostly 2–2½ cm wide, slightly narrowed at the base, especially on the acroscopic side, gradually and strongly narrowed from the middle to the apex, upper pinnae somewhat shortened, the terminal about the size of the lower ones. Secondary rachises stramineous to (mostly) reddish-brown, abaxially terete at the base, becoming angular (mostly gradually) at the level of the 1st–4th pinnule, mostly sulcate above, the margins not or hardly paler. *Pinnules* ca. 10–35 to a side, almost always alternate, spreading or often somewhat ascending, subsessile, (7–)9–18 mm long, (3–)4–7 mm wide, a strongly reduced axillary pinnule usually present, a few additional basal ones, especially on the acroscopic side, slightly reduced. Inner margin straight, often touching or slightly overlying the sec. rachis, lower base cuneate, hardly stalk-like, upper base subangular or very shortly rounded, upper margin straight in the inner, convex in the outer part, lower margin straight or often slightly concave, apex rounded or narrowed-subacute, or angular at the basiscopic side, a separate outer margin often ± developed, the pinnules mostly distinctly but not very strongly narrowed to the apex, widest at the base. Marginal thickening pale, inconspicuous. Upper/outer margin subentire to erose-denticulate or slightly crispate in fertile pinnules, crenate-dentate, often with acute teeth, in sterile ones. Vein-ends ca. ¾–1½ mm apart; main vein hardly united with the marginal strand, ca. 0.4 mm above it near the apex. Upper pinnules gradually and strongly reduced, the highest denticuliform, 2–4 mm long, several confluent with the terminal segment which is narrowly lanceolate to linear, subacute or obtuse, crenate-lobed at the base, ½–2 cm long, rarely caudate and up to 3 cm long, sterile or soriferous in the basal lobes. Indusium pale, delicate, 0.2–0.3 mm wide, erose-denticulate to subentire, not reaching the margin by a distance of 0.1–0.4 mm, strongly reflexed and conceiled at full maturity. Sporangia ca. 132 × 95 μ; annulus with 11–14 indurated cells; spores monolete, bean-shaped, hyaline, almost colourless, ca. 16 × 25 μ.

Distribution: South-eastern Brazil (map 16). Im moist forests, sometimes along watercourses, at lower altitudes (few data extant).

Representative specimens:

BRAZIL. MINAS GERAIS: Viçosa, Cha-Cha-valley, Mexía 4410a (UC, US); São Sebastião do Paraiso, Brade, Altamiro & Teodoro Ba 77 (GH); São João Nepomuco, Lopes s.n. (RB).

RIO DE JANEIRO: Near Rio, Raddi s.n. (PI, HOLOTYPE, 3 sheets; Isotypes in FI, G, K, P); ibid., Forssell 225, 231 (S-PA); Corcovado, Glaziou 1653 (BR); ibid., Lindman A 165 (S, S-PA); Serra dos Orgãos, Miers 135 (NY); Catumby, Mosén 73 (C, K, LE, S).

SÃO PAULO: Campinas, Severin 48 (B, BR, FI, M, S, S-PA, UPS); Alto da Serra, L. B. Smith 1965 (GH); Iguapé, Brade 8226 (BM, US); Cajures, Brade 8262 (S-PA).

PARANÁ: Serra da Prata, Dusén 15298 (B, S, S-PA, US).

The dark axes, gradually reduced upper pinnules with small terminal segment, and monolete spores characterize this subspecies. It is closely related to ssp. *terminalis*, which has trilete spores and usually less reduced upper pinnules with a larger terminal segment, and to *L. pallida*, where the differences are pointed out.

c. ssp. **terminalis** Kramer, ssp. nov. **Fig. 49**

Petiolus atrofuscus vel atratus, quadrangularis, vel facie abaxiali obtuse angularis vel subteres; lamina bipinnata, rhachidibus obscuris, secundariis facie abaxiali inferne subteretibus, superne angularibus vel sulcatis; pinnulis herbaceis, atrovirentibus vel olivaceis, superioribus plerumque paullum redactis, segmento terminali magno, late lanceolato, pinnulis superioribus vix iuncto; indusio pallido, angusto, 0.15

mm lato, leviter eroso-crenulato, marginem non attingente; sporis tetraedriformibus.

Typus: Lindman A 1757 from Colonia Presidente Gonzalez, Paraguay (S).

Petioles ca. 1 mm in diam. near the apex, ± shining, subterete at the extreme base, otherwise quadrangular, or abaxially mostly obtusely angular to subterete, the adaxial surface, sometimes also the others, sulcate. *Lamina* with 2–7 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, mostly obtusely angular on the abaxial side, the edges of the adaxial groove pale, somewhat wing-like, sometimes extending to the upper part of the petiole. *Pinnae* subopposite, the upper alternate, subsessile, the lower ones ca. 3–4 cm apart, laxly ascending under an angle of 30–40°, the largest 12–15 cm long, 2–3(–3½) cm wide, widest just below the base or in the basal one-third or half, slightly narrowed at the base, gradually and more strongly narrowed towards the apex, the upper ones somewhat shortened and closer. Terminal pinna often widest, stalked (1–2 cm). Secondary rachises at least at the base brownish to blackish-brown, adaxially broadly and shallowly grooved, the borders somewhat pale and wing-like, abaxially subterete or terete at the base, gradually obtusely or sharply angular above, mostly not sulcate or near the apex only, occasionally angular almost throughout. *Pinnules* 10–20 to a side, mostly alternate throughout, usually somewhat ascending, subsessile, 11–16 mm long, 5–7 mm wide, a strongly reduced axillary pinnule mostly present, a few additional ones often somewhat reduced. Inner margin straight, approximately parallel to the sec. rachis, lower base cuneate, hardly stalk-like, upper base angular or shortly rounded, lower margin straight or often slightly convex towards the apex, upper margin straight at the base, strongly convex towards the apex which is subacute or shortly rounded; pinnules rather strongly narrowed towards the apex, a separate outer margin hardly developed. Marginal thickening narrow, pale, inconspicuous. Upper margin shallowly crenate to sinuous in sterile pinnules, minutely erose to subentire, sometimes slightly crispate in fertile ones. Vein-ends ca. 1–1½ mm apart; main vein hardly united with the marginal strand, ca. ½ mm above it near the apex. Upper pinnules not strongly reduced, ca. 5–10 cm long, one or two connected by a narrow wing with the terminal segment which is rather large, 1–2 cm long, broadly lanceolate, with two unequal basal, often soriferous lobes, subacute to obtuse, the central shank shallowly sinuate-crenate; rarely the upper pinnules are more strongly reduced and the terminal segment is small. Indusium not reaching the margin by a distance equal to about twice its width, strongly reflexed and conceiled at full maturity. Sporangia ca. 165 × 125 μ; annulus with 7–11 indurated cells; spores very pale brownish-yellow, ca. 25 μ.

Distribution: South-eastern Brazil and Paraguay (map 15). In similar localities as the preceding subspecies, not rarely collected together with it.

Representative specimens:

BRAZIL. RIO DE JANEIRO: Maná, Schreiner 18468 (NY).

SÃO PAULO: Sorocaba, Mosén 3733 (S, S–PA, UPS); Iguapé, Bõa Vista, Brade 7727 (UC); Alto da Serra, Wacket s.n. (Rosenstock-exs. 348) (B, M, NY, S, S–PA, UC, US, W); São José dos Campos, Löfgren 422 (S); Rio Grande, Edwall 4967 (S–PA); Moóca, Brade 5386 (S–PA); Alto da Serra, Wacket 16 (S–PA); Santos, Regnell s.n. (UPS).

PARANÁ: Serra da Prata, Dusén 15298 in part (BR, S); Volta Grande, Dusén 14139 in part (B, S, US), 11439 (S).

SANTA CATARINA: Itajaí, Reitz 3974 (US); Blumenau, Heins 13 in part (US); Joinville, Ule 37 (B); ibid., Schmalz 25 in part (F, MO, S–PA).

RIO GRANDE DO SUL: Porto Alegre, Stier 280 (S–PA); near São Leopoldo, Eugenio 48 (NY).

PARAGUAY: Colonia Presidente Gonzalez, Lindman A 1757 (S, HOLOTYPE; Isotypes in BM, G, GH, K, S, S–PA, UPS, US); Central Cordillera, Upper Río Y-acá, Hassler 6732 (B, BM, G, K, S–PA).

Most closely related to the preceding subspecies: aberrant specimens of ssp. *terminalis* with small upper pinnules and small terminal segment can only safely be distinguished by the spore-shape. Other relatives are *L. divaricata*, which is often very close, especially specimens with less distinctly developed wings on the axes occurring in Paraguay and southern Brazil, *L. lancea*, and *L. guianensis* ssp. *lanceastrum*, to which species the reader is referred.

d. ssp. **antillensis** Kramer, ssp. nov. **Fig. 53, 54**

L. montana Fée, 11^{e} mém. 17 (1866), in part (*nomen confusum*, see p. 343); Duss, Fl. Crypt. Ant. franc. 58 (1904); Hieronymus, Hedwigia 62:15 (1920); Maxon, Pterid. Port. 489 (1926); Domin, Pterid. Domin. 244 (1929); Stehlé, Caribb. For. 4 (2): 92 (1943); Hodge, Lloydia 17 (2):102 (1954). Type: L'Herminier s.n. from Guadeloupe (P!, consisting partly of *L. guianensis* ssp. *guianensis*).

Homotypic synonyms: *L. lancea* (L.) Bedd. f. *montana* (Fée) Lindman, Ark. f. Bot. I:198 (1903), as to type only.

L. lancea (L.) Bedd. var *montana* (Fée) Bonaparte, Notes Ptérid. VII:343 (1918), X:202 (1920).

Misapplied name: *L. trapeziformis* auct. non Dryander; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. mai.

Petiolus stramineus vel pallide fuscus, facie abaxiali inferne tereti vel subtereti, superne angulari vel interdum etiam subtereti; lamina bipinnata, herbacea, rhachidibus secundariis stramineis, facie abaxiali basi infima tereti, deinde subito canaliculata, marginibus nunquam alatis; pinnulis linguiformibus vel rotundato-subrhomboideis, apice plerumque late rotundatis, pinnulis superioribus sensim redactis; indusio pallido, integro vel subintegro, 0.2-0.3 mm lato, marginem subaequante vel breviore; sporis tetraedriformibus.

Typus: Eggers 647 from Roseau-lagoon, Dominica (B).

Petioles ¾–1¼, mostly 1 mm in diam. near the apex, dark brown at the base, there subterete, otherwise stramineous to pale (rarely medium) brown, adaxially sulcate close to the base or flattened below. *Lamina* with 1–4 primary pinnae to a side and a conform terminal one, very rarely simply pinnate. *Primary rachis* abaxially flattened or sulcate, less often subterete below or throughout. *Pinnae* subopposite, the upper ones mostly alternate, subsessile, the lower ones 2½–7 cm apart, the upper ones gradually closer, laxly ascending under an angle of ca. 30–50°, the largest 9–25 cm long, 1.5–3(–3.5) cm wide, widest somewhat above the base, slightly narrowed towards the base, very gradually narrowed to the apex, the upper ones little or not shortened, the terminal pinna sometimes largest, with a stalk up to 2 cm long. Secondary rachises adaxially narrowly and deeply sulcate, abaxially with a short terete basal portion, from the level of the 1st–3rd pinnule abruptly sulcate. *Pinnules* ca. 15–40, mostly about 25, to a side, alternate or the lower or medium ones subopposite, spreading or slightly ascending, rarely decurved, or subfalcate, the largest 12–18, mostly ca. 13 mm long, 5–8, mostly 6 mm wide, widest at the base, but little narrowed to the broadly rounded apex, less often more strongly narrowed or of equal width throughout. Inner margin straight, parallel or slightly divergent from the rachis, lower base shortly cuneate, hardly stalk-like, upper base subangular or shortly rounded, lower margin straight or faintly concave, convex, or S-shaped, upper margin straight in the inner, convex in the outer part, less often more evenly convex throughout. Marginal thickening stramineous, inconspicuous except along the lower edge. Upper/outer margin entire in fertile pinnules, sinuate or distantly crenate, with incisions up to 1 mm deep and rounded teeth in sterile ones which are not very rare. Vein-ends 1–1½ mm apart; main vein only shortly connected with the marginal strand, ca. 0.5 mm above it near the apex. Upper pinnules gradually reduced, the highest ca. 3–5 mm long, 1–3 connected by a wing with the terminal segment, which is lobed-triangular to narrowly lanceolate, obtuse, ½–3 cm long, sterile except in the basal lobes. Indusium almost equalling the margin or falling short of it by its own width, ± reflexed at full maturity. Sporangia ca. 160 × 125 μ; annulus with 9–12 indurated cells; spores pale brownish-yellow, ca. 28 μ, 16?

Distribution: Puerto Rico and Lesser Antilles, sometimes incorrectly ascribed to other regions (as *L. montana*), apparently commonest in Dominica and Guadeloupe; also on the Paraguaná-Peninsula, Venezuela (map 17). In dense rainforests and elfin woodland, mostly terrestrial, occasionally on tree-trunks, from ca. 300–1100 m (rarely lower).

Representative specimens:

PUERTO RICO: Sierra de Naguabo, Barrio de Maizales, Britton & Hess 2290 (F, NY, S, US); Adjuntas, Mt. Andubo, Sintenis 4675 (B); Adjuntas, Las Cruces, Sintenis 4051 (B, BM, G, GH, GOET, L, LE, M, MO, S–PA, US); Peñuelas, Las Cruces, Sintenis 4374 (B, US); Sierra de Luquillo, Blauner 293 (BM, G).
GUADELOUPE: Husnot 272 (BM, BR, F, FI, G, K); Questel 1848, 3031, 3273 (US); Duss 4239 (NY), 4243 (NY, US); Stehlé 521 (F, US), 2419 (US); L'Herminier 42, 44 in part (B, BR, G, GOET, K, P, W); id. s.n. in part (P, HOLOTYPE of *L. montana*; other authentic specimens in B, BM, G, K, L, LE, MO, NY, P, US).
DOMINICA: Eggers 647 in part (B, HOLOTYPE; Isotypes in B, G, GOET, L, LE, W); Jenman s.n. (NY); Lloyd 213 (NY, US); Hodge 66, 1119 (GH, NY), 1219, 1386, 2281 (GH); Hodge & Hodge 1713, 1914, 2620 (GH).
MARTINIQUE: Duss 1707 (F), s.n. (B, F, M, US).
ST. LUCIA: Box 429 (BM, US), 1705 (BM); Day 390 (B), Murray s.n. (K).
ST. VINCENT: H. H. & G. W. Smith 1893 (BM); Arnott s.n. (NY).
GRENADA: Eggers 6191 (GOET, L, US); Beard 1309 (GH, MO, S, US); Broadway s.n. (F, GH, MO, NY, US); Jenman s.n. (NY); Sherring s.n. (G, NY, US).
VENEZUELA. FALCÓN: Paraguaná-Peninsula, Cerro Santa Ana, Curran & Haman 681 (GH, NY).

L. quadrangularis ssp. *antillensis* is not as closely allied to the other subspecies as those are among each other, and deserves perhaps recognition as a species. Otherwise it is rather close to *L. lancea*, but that species differs in almost always much less reduced upper pinnules and larger, free terminal segment, and by the apex of the pinnules wich is angular at the basiscopic side. The reason for rejecting Fée's name *L. montana* is explained on p. 343.

The subspecies of *L. quadrangularis* are clear-cut and rather distinct and there would be hardly any serious objection against treating them as separate species, particularly ssp. *antillensis*.

L. quadrangularis can be said to occupy a central or perhaps rather a basal position in the section *Lindsaea*, as it is related to several, rather diverse species probably representing separate lines of evolution: *L. lancea*, *L. divaricata*, *L. arcuata*, *L. pallida*, *L. guianensis*, possibly also *L. portoricensis*.

15. **Lindsaea pallida** Klotzsch, Linnaea 18:547 (1884); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Hieronymus, Hedwigia 62:17 (1920). **Fig. 52**

Type: Schomburgk 1205, British Guiana (B!).

Heterotypic synonym: *L. lancea* f. *marginalis* Lindman, Ark. f. Bot. I:199 (1903), pl. 8 fig. 3. Type: Lindman A 3341 ½ from Serra do Itapirapuan, Matto Grosso, Brazil (S!).

Misapplied names: *L. quadrangularis*, *β*, of Hooker, Spec. Fil. I:214 (1844); Kunze, Bot. Zeit. 8:346 (1850).

L. quadrangularis auct. non Raddi; Fée, Crypt. vasc. Brés. I:29 (1869), in part; Posthumus, Fl. Surin. Suppl. 75 (1928).

L. trapeziformis auct. non Dryand.; Baker, Fl. Bras. I^2:355 (1870), in part.

Petioles pale, abaxially obtusely angular to subterete; lamina bipinnate with conform terminal pinna, chartaceous; pinnules rounded-trapezoidal or dimidiate-ovate, ca. 2 × as long as wide, the upper ones gradually reduced; sterile upper/outer margin with small acute teeth; sori continuous; indusium strongly and irregularly erose-denticulate; spores monolete.

Rhizome creeping, 2–2.5 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.7 mm long and 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* rather close, ca. 10–40 cm long, about as long as to 1½ × the length of the lamina, (¾–)1–1.5 mm in diam. at the base of the lamina, ± shining, adaxially in the upper part with a deep narrow groove which often evanesces downwards, the lower half more flattened to subterete. *Lamina* bipinnate (very rarely with a few subbipinnate primary pinnae), ca. 15–30 cm long, rather bright green to olive on the ventral, paler on the dorsal side, with 2–6 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially often sulcate above. Axillary cushions indistinct, hardly ever discoloured. *Pinnae* mostly subopposite, laxly ascending under an angle of ca. 40–60°, subsessile, the lower up to 5 cm apart, the upper closer, 9–18 cm long, the upper ones about ⅔ of the length of the lower, 1.5–3.5, mostly 2–3 cm wide, widest somewhat above the base which is slightly narrowed, the upper part gradually narrowed to the long-acuminate apex. Secondary rachises stramineous, slender, adaxially with a deep narrow groove the thick borders of which often touch, abaxially terete at the base, then becoming gradually angular to shallowly sulcate, the terete part occupying ⅓ or ¼, occasionally less, of the length; rachis of terminal pinna abaxially sulcate throughout. *Pinnules* ca. 15–25 to a side, alternate, spreading or mostly somewhat ascending, 8–20 mm long, 5–10 mm wide, widest at base, the apex but little narrowed, broadly rounded. The pinnules are in shape approximately intermediate between the most common form of *L. lancea* and *L. quadrangularis*, resembling large forms of *L. stricta* f. *moritziana*. Lower base cuneate, hardly or not stalk-like, upper base shortly rounded to almost angular, inner margin approximately straight, parallel or mostly slightly touching to overlying the secondary rachis; upper margin straight or faintly convex at the base, more strongly convex towards the apex, lower margin straight to very faintly S-shaped, convex at the extreme apex; upper edge minutely but distinctly erose-denticulate when fertile, when sterile (in normally fertile leaves the tips of the apical pinnules are usually sterile) with acute uninerval teeth up to ½ mm long. Marginal thickening stramineous, indistinct except at the base of the basiscopic edge. Upper pinnules gradually reduced, the apical ones denticuliform, 1–2 mm long, strongly ascending, confluent into a narrowly lanceolate caudate-acuminate apical segment 1.5–2.5 cm long, acute or subacute, lobed at the base, the lobes mostly sterile and sharply denticulate. Veins immersed, obscure, mostly twice forked, rather close, their ends about ½–¾ mm apart; main vein hardly united with the marginal strand, ca. 0.3 mm above it near the apex. *Sori* along the upper/outer margin; indusium stiff, greyish, 0.4–0.6 mm wide, not reaching the margin by 0.2 mm to almost equalling it, little or not reflexed at full maturity. Sporangia 155–160 × 115–120 μ; annulus with 12–14 indurated cells; spores bean-shaped, very pale brownish, ca. 24 × 36 μ.

Distribution: Venezuela, Trinidad, Guiana, northern, central, and eastern Brazil; apparently uncommon (map 18). Terrestrial, collected in forests and campos; very few ecological data extant.

VENEZUELA. MIRANDA: El Hatillo, Br. Ginés 211 (US).
TRINIDAD: St. Ann's Hill, Trin. Bot. Gard. Herb. 102 in part (US); without loc., id. 103 (US).
BRITISH GUIANA: Potaro R., Jenman s.n. (NY); Humirida Mts., Appun 1259 (K); prob. the same coll., Glaziou 12356 (B, BR, C, G, LE, NY); without loc. Schomburgk 1205 in part (B, HOLOTYPE; Isotypes in B and BM).
FRENCH GUIANA: Oyapok, Leprieur (?) s.n. (K); without loc., Leprieur 164 in part (B, G, P).
BRAZIL. AMAZONAS: Toê-câ, Igarapé, von Lützelburg 21520 (M, UC).
RIO BRANCO: Igarapé, Rio Quinô, von Lützelburg 21364 (M).
PERNAMBUCO: Catucá, Gardner 1225 (K); near Macacos, Ridley, Lea & Ramage s.n. (BM).
BAHIA: Jacobina, Blanchet s.n. (G); without exact loc., Blanchet s.n. (G).
MATTO GROSSO: Serra do Itapirapuan, Affonso, Lindman A 3341 1/2 (S; HOLOTYPE of *L. lancea* f. *marginalis* Lindman).
COLOMBIA?: "New Grenada", Linden 708 (BR, K).

This species is most closely allied to *L. quadrangularis* ssp. *quadrangularis*, from which it differs mainly in pale axes and more strongly erose indusium and fertile margin. The general shape of pinnae and pinnules, the sharply incised sterile margin, and the monolete spores (otherwise not found in the present section) are points of similarity. It is strange that this species, which, though not very outstanding in appearance, can easily be told apart by the above-mentioned characters, has become almost obsolete after its original publication. Specimens in herbaria are generally referred to *L. stricta* (because of pale colour and obscure veins) or *L. quadrangularis*. Its distribution seems to be still very insufficiently known.

16. **Lindsaea arcuata** Kunze, Linnaea 9:86 (1835); Hooker, Spec. Fil. I:215 (1846); Kunze, Farrnkr. II:46; t. 119 (1850); Bot. Zeit. 8:369 (1850); Ettingshausen, Farnkr. 212; t. 146 fig. 23 (1865); Hieronymus, Hedwigia 47:209 (1908); Rosenstock, Fedde Rep. 11:60 (1912); Hieronymus, Hedwigia 62:15 (1920); C. Christensen, Kgl. Sv. Vet.—Akad. Handl. Ser. 3, 16 (2): 46 (1937); not of Jenman, W. Ind. Gui. F. 74 (1899). **Fig. 55**

Type: Poeppig 1133 from Pampayaco, Perú, prob. destroyed in LZ; Isotype (?) in B!
Homotypic synonyms: *L. trapeziformis* Dryand. var. *β arcuata* (Kze.) Baker, Fl. Bras. I²: 355 (1870), as to part of cited specimens only; t. 21 fig. 20, 21, t. 22 fig. 2.
L. lancea (L.) Bedd. var. *arcuata* (Kze.) Rosenstock, Hedwigia 46:80 (1906).

Heterotypic synonyms: *L. horizontalis* Hooker, Spec. Fil. I:214 (1844), pl. 62 B; Kunze, Bot. Zeit. 8:347 (1850); Kunze, Farrnkr. II:47 (1850); Seemann, Bot. Voy. Herald 239 (1854); Fée, Crypt. vasc. Brés. I:29 (1869); J. Smith, Hist. Fil. 268 (1875). Lectotype: Gardner 157 from Serra dos Orgãos, Rio de Janeiro, Brazil (K!).

Homotypic synonyms: *L. trapeziformis* Dryand. var. *horizontalis* (Hook.) Grisebach, Catal. Plant. Cub. 274 (1866).

L. lancea (L.) Bedd. var. *horizontalis* (Hook.) Losch, Mitt. Bot. Staatss. München 1:23 (1950).

L. dolabra Kunze, Farrnkr. 2:47 (1849); Bot. Zeit. 8:370 (1850). Type: Funck & Schlim 598 from the state of Carabobo, Venezuela, prob. destroyed in LZ; Isotypes in BM, G, M!

L. curvans Fée, Gen. Fil. 106 (1852), Crypt. vasc. Brés. I:30 (1869), II:20 (1872/73). Type: Galeotti 6489 from the state of Oaxaca, Mexico, (P!).

L. Galeottii Fée, Gen. Fil. 107 (1852). Type: Galeotti 6469 from the state of Oaxaca, Mexico (P!).

L. Kunzei Moritz in Ettingshausen, Farnkr. t. 147 fig. 7 (1869). Type: not indicated; a specimen with authentic annotation agreeing very well with Ettingshausen's plate should be regarded as type: Moritz 454 from Tovar, state of Mérida, Venezuela (B!).
Homotypic synonym: *L. trapeziformis* Dryand. f. *kunzei* (Moritz) Kümmerle, Mag. Bot. Lap. 13:37 (1914).

L. lancea (L.) Bedd. var. *angulata* Rosenstock, Fedde Rep. 22:6 (1925). Type: Brade 317 from Carillo, Costa Rica (S-PA!).

Misapplied names: *L. quadrangularis* auct. non Raddi; Mettenius, Ann. sci. nat. V, 2:217 (1864). *L. trapeziformis* auct. non Dryander; Christ in Pittier, Prim. Fl. Costar. 3:38 (1901); probably also of Rovirosa, Pteridogr. Mex. pl. IX (1909).

L. lancea (L.) Bedd. var. *montana* (Fée) Bonaparte of Losch, Mitt. Bot. Staatss. München 1:24 (1950); not *L. montana* Fée.

Petioles stramineous to pale brown; lamina bipinnate with conform terminal pinna or simply pinnate, herbaceous; pinnules very variable in shape, acute or truncate, 3–3½ × as long as wide, the upper ones gradually reduced; sori continuous; indusium narrow, subentire; spores trilete.

Rhizome creeping, often long and with numerous short branches, (1.5–)2–4 mm in diam.; scales lanceolate, acute-acuminate, up to 1 mm long and 0.2 mm wide, with up to 6 rows of cells at the base. *Petioles* rather remote to densely clustered, (7–)12–ca. 40 cm long, from half to twice as long as the lamina, mostly of approximately equal length, ¾-2 mm in diam. near the apex, often considerably stouter at the base, abaxially flattened below, broadly and shallowly grooved above, abaxially angular above, obtusely angular to subterete below, often sharply angular almost to the base, occasionally obtusely angular or subterete throughout. *Lamina* dark to medium green, paler on the dorsal side, ca. 10–45 cm long, with 1–3, occasionally up to 8 pinnae to a side and a conform terminal one when bipinnate. *Primary rachis* adaxially broadly and shallowly sulcate, abaxially sharply angular and often sulcate, less often subterete or terete. Axillary cushions mostly visible as slight swellings. *Pinnae* (if any) subopposite or alternate, mostly subsessile, the terminal distinctly stalked (up to 3 cm), forming a rather variable angle with the primary rachis but mostly ascending (ca. 30°), rather far apart, ca. 3–6 cm, ca. 10–35 cm long, (2.5–)3–7 cm wide, the terminal often largest, especially in paucijugate leaves, mostly widest just above the base, slightly narrowed at the base, from the widest point gradually, close to the apex more strongly narrowed. The same applies mutatis mutandis to simply pinnate laminae. Secondary rachises adaxially with a rather narrow groove, abaxially subterete at the base, from the level of the second or third pinnule angled, the angles not or hardly paler, not wing-like, the surface between them shallowly concave or flat; rachis of terminal

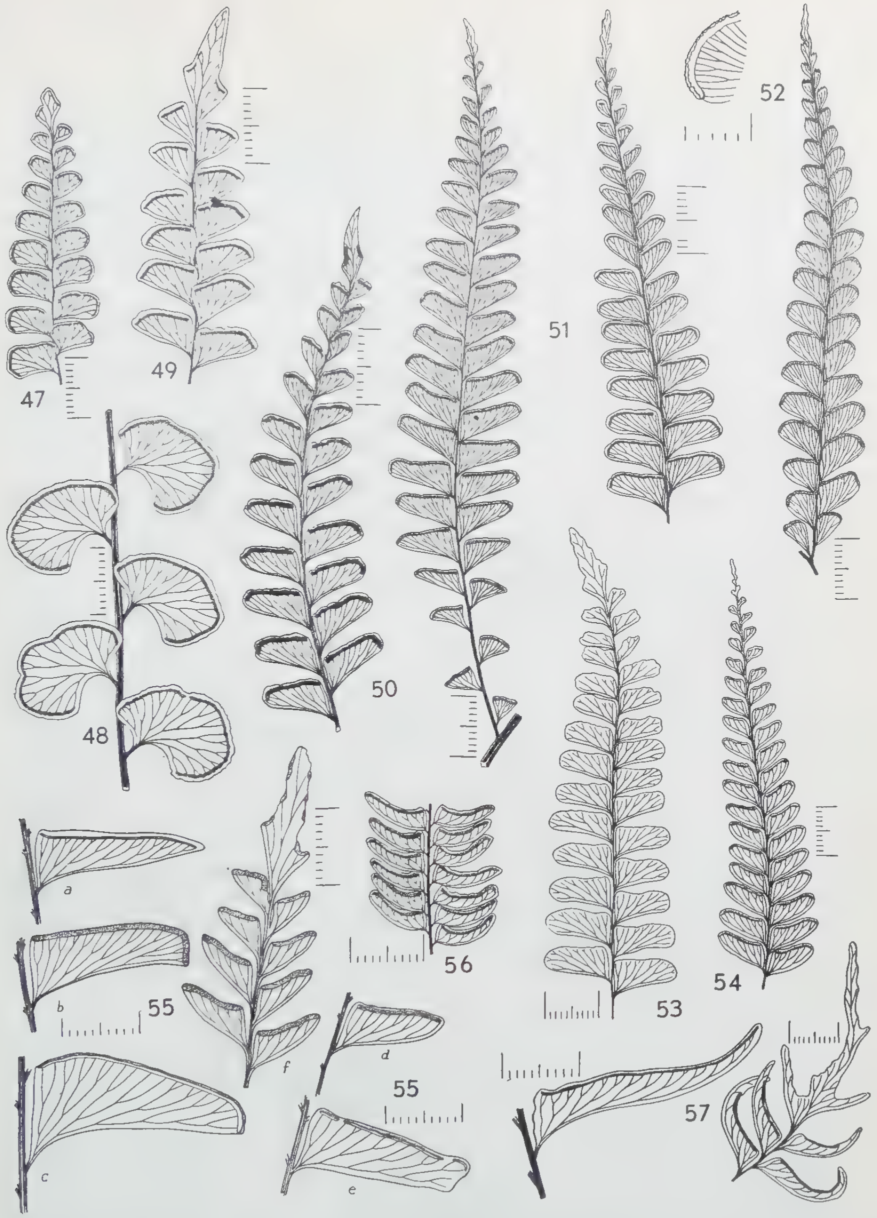


Fig. 47–48: *Lindsaea botrychioides;* fig. 47: apex of lamina; fig. 48: middle pinnules (Dusén 8334). Fig. 49: *L. quadrangularis* ssp. *terminalis;* apex of upper pinna (Mosén 3733). Fig. 50: *L. quadrangularis* ssp. *subalata;* apex of upper pinna (no coll.). Fig. 51: *L. quadrangularis* ssp. *quadrangularis;* middle pinna (left) and upper half of lower pinna (right) (Dusén 15298). Fig. 52: *L. pallida;* upper pinna and apex of pinnule (left) (Appun s.n., Glaziou 12356). Fig. 53–54: *L. quadrangularis* ssp. *antillensis;* fig. 53: apex of sterile terminal pinna (Eggers 647); fig. 54: apex of fertile terminal pinna (Booth s.n.). Fig. 55: *L. arcuata;* a-e pinnules of bipinnate leaves (a: Wallis s.n., b: Donnell Smith 6022, c: Moritz 454, d: Burchell 2457, e: Wright 976); f: apex of basal pinna (Donnell Smith 6022). Fig. 56: *L. spruceana;* basal portion of simply pinnate lamina (Spruce 4023). Fig. 57: *L. coarctata;* left: pinnule from middle pinna; right: apex of middle pinna (Schultes & Cabrera 15308). (Scales in mm).

pinna and of simply pinnate laminae angular or sulcate throughout. *Pinnules* 20–35(–50) to a side, the upper ones alternate, the lower ones mostly subopposite, subsessile, spreading or ± ascending, occasionally slightly deflexed, rather close but not contiguous, very variable in shape (see fig. 55), (12–)15–35 mm long, (4–)5–11 mm wide, of equal or almost equal width throughout or more often rather strongly narrowed towards the apex, and by this character separable in two forms: one with truncate, the other with ± acute, narrowed apex, which, however, are connected by numerous intermediates. Inner margin straight and then parallel, or often convex above and then touching or overlying the rachis, lower base cuneate, hardly stalk-like, upper base angular, rarely subauriculate, lower margin mostly shortly concave at the base, otherwise straight or shortly concave at the apex again (in truncate pinnules which are sometimes hamate at the apex) or there slightly convex, more strongly in pinnules with acute upturned apex (e.g. in the type-specimen, whence the name *arcuata*) upper margin straight or slightly convex throughout and parallel to the lower in truncate pinnules, often shortly convex or concave in acute ones; an outer margin only developed in truncate ones. The acute form is more common than the truncate one; the two are but rarely found together on a single leaf. Marginal thickening stramineous, inconspicuous, except at the base of the lower margin. Upper/outer margin entire or minutely erose in fertile pinnules, shallowly sinuate-crenate in sterile ones which are very rare. Veins immersed, mostly twice forked, lax, their ends ca. 1–1 ½ mm apart; main vein hardly connected with the marginal strand, ca. ½ mm above it near the apex. Upper pinnules gradually but not very strongly reduced, the highest ca. 5 mm long, one or two connected by a wing with the terminal segment which is lanceolate, cuneate at the base, with two unequal basal teeth or lobes, obtuse or subacute at the apex, ca. 1–2 mm long; sometimes the upper pinnules are much more gradually reduced, several denticuliform ones passing into a sometimes caudate terminal segment (especially in Central American, Cuban, and Brazilian specimens). *Sori* along the upper/outer margin; indusium greenish or pale, ca. 0.2 mm wide, not reaching the margin by a distance equal to its own width or less, reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ; annulus with 10–13 indurated cells; spores very pale brown, ca. 22–27 μ.

Distribution: Cuba, Hispaniola, Mexico to Bolivia, and southeastern Brazil (erroneously reported from Grenada by Baker, Ann. Bot. 6:97, 1892) (map. 21) In forests, sometimes in clearings or along streams, from ca. 1000 to 2000 m (rarely lower, near the southern limit of its range).

Representative specimens:

Cuba. Oriente: Near Monte Verde, Wright 976 in part (B, BM, BR, F, G, GH, GOET, K, L. NY, PH, S–PA, UC, US); Pinales de Monte Verde to Falls of Río Palenque, Shafer 8861 (NY); Santa Ana, north of Jagüey, Yateras, Maxon 4180 (NY, S–PA, US).

Hispaniola. Haïti: Massif de la Hotte, w. group, Torbac, Morne Formond, Ekman H 7427 (C. Chr. in BM, K, S, US); ibid., Jérémie, Morne de l'Etang, Ekman H 10380 (B, C, K, S, US).

Mexico. Oaxaca: Without loc., Galeotti 6469 (P, Holotype of *L. Galeottii*); id., Galeotti 6489 (P, Holotype of *L. curvans*).

Guatemala: Near Finca Sepacuite, Alta Verapaz, Cook & Griggs 857 (US); Pansamalá, ibid., von Türckheim s.n. (Donnell Smith-exs. 830) (B, GH, K, NY, UC, US).

Costa Rica: Cartago, Cooper s.n. (Donnell Smith-exs. 6023) (B, G, GH, K, M, NY, US); Estrella, Cooper s.n. (Donnell Smith-exs. 6022) (B, F. G, GH K, MO, NY, US); s. of Cartago, along Pan-American Highway, Chrysler 5456 (MO, UC); Finca Navarro, Maxon 645 (NY, US); Navarrito, Lankester 751 (S–PA, US).

Panamá: Mt. Pirri, prov. Panamá, Goldman s.n. (US).

Colombia. El Valle: La Cumbre, Killip 5914 (GH, NY, US); Monte Frío, Yamacones, Killip & García 33709 (US).

Cauca: La Gallera, Micay Valley, Killip 7778 (PH, US); w. slopes of Cali-Cordillera, Lehmann 3003 (BM, G).

Norte de Santander: Salazar, Engel s.n. (LE).

Santander: Ocaña, Schlim 606 (BR, G, FI, K, L). Las Cruces, Kalbreyer 938 (B, K); Mesa de los Santos, Eastern Cordillera, Killip & A. C. Smith 15129 (NY, US).

Antioquia: Cineguetas, Kalbreyer 1872 (B, K).

Huila: E.s.e. of Garzón, Fosberg 19899 (US).

Meta: W. of Villavicencio, between R. Manzanares and Quebrada Playón, Grant 10101 (US).

Venezuela. Mérida: Near Tovar, Moritz 454 (B, Holotype of *L. Kunzei*; Isotypes in BM, GH, L, UPS).

Carabobo: Without loc., Funck & Schlim 598 (BM, G, M, Isotypes of *L. dolabra*).

Ecuador: Without exact loc., e. part of the country, Gardini 78 (Pic.-Ser.).

Perú. Junín: Pichis Trail, Yapas, Killip & A. C. Smith 25522 (F, NY, US).

Loreto: Tierra Doble on R. Nanay, Ll. Williams 1071 (F, US).

Dept.?: Pampayaco, Kanehira 177 (GH, US).

Bolivia. La Paz: Hacienda Simaco above road to Tipuani, Buchtien 5116 (GH, S–PA, UC, US); San Carlos near Mapiri, Buchtien 1098 (S–PA, US); Hacienda Casana, Tipuani-Valley, Buchtien 7028 (G, GH, NY, S–PA).

Brazil. Minas Gerais: Capão Redondo near Lagoa Santa, Warming 59 (C); Ouro Preto, Morro São Sebastião, Damazio s.n. (RB); without loc., de Moura s.n. (B).

Rio de Janeiro: Upper Macahé, Mendonça 414 (B); Serra d'Estrella, near Petropolis, von Lützelburg 13750 (M); ibid., Ohaus s.n. (US); Serra dos Orgãos, Gardner 157 (K, Lectotype of *L. horizontalis;* Isotypes in BM, FI, W); ibid., Burchell 2457 (B, K); Theresopolis, Frazão 2120 (US); ibid., Brade 9368 (NY).

São Paulo: Paranapiacaba, Brade 8412 (UC); Serra do Mar, Lüderwaldt 1426 (S–PA); Alto da Serra, Hoehne 1224 (BM); ibid., L. B. Smith 1965 (GH).

Santa Catarina: Piraí, Schmalz s.n. (US); Serra do Quiririm, Schmalz 83b (S–PA).

In spite of the very variably shape, *L. arcuata* can be recognized by the great relative length of the pinnules, a character shared with *L. spruceana* which is perhaps not distinct (see there). Otherwise the closest relative of *L. arcuata* is *L. quadrangularis*. Certain Central American specimens of *L. arcuata* are very close to *L. qu.* ssp. *subalata*, from which they can be distinguished by more elongate pinnules and paler axes, and to ssp. *antillensis*, which has relatively shorter, more rounded pinnules. A few specimens are, however, more or less intermediate between the two species.

Some specimens, notably from Central and northern South America have pinnules with a more or less protracted apex that points obliquely upwards, not unlike those of *L. herminieri*. One of these specimens has been described as *L. lancea* var. *angulata* Rosenstock. Examples of this form are Killip & Garcia 35627 (US) from Buenaventura, El Valle, Colombia, Brade 317 (S-PA, Holotype of *L. lancea* var. *angulata*, Isotype in NY) from Carillo, Costa Rica, Kalbreyer 1872 (B) from Cineguetas, Antioquia, Colombia, Buchtien 44 (S-PA) from Mapiri, Bolivia, and, the most extreme specimens, with caudate apices up to 3½ cm long, Killip 5276 (NY, PH, US) from Cordoba, El Valle, Colombia. Two specimens from Suriname, where *L. arcuata* has never been found, are referred with misgivings to this form: B.W. 321 and 599 (U) from Brownsberg; they have been included by Posthumus (1928) in *L. herminieri;* the reasons for excluding them from that species have been explained there. Extreme specimens of the caudate form can be distinguished from *L. taeniata* by closer pinnules and by the sterile outer margin (lower margin of the apex), which is soriferous in that species. They are not distinguished here as a separate form, because they gradually pass into the normal form of *L. arcuata* through a series of intermediates, and caudate and non-caudate pinnules are often found together on one leaf.

17. **Lindsaea spruceana** Mettenius ex Kuhn, Linnaea 36:79 (1869); Hooker & Baker, Syn. Fil. 2nd ed. 108 (1874); Kuhn, Chaetopt. 26 (1882); Christ. Farnkr. d. E. 293 (1897); Diels. N. Pfl. I⁴:221 (1902). **Fig. 56**

Type: Spruce 4023 from Mt. Guayrapurima near Tarapoto, San Martín, Perú (B!).

Homotypic synonym: *L. tarapotensis* (lapsu: *tarapotense*) C. Christensen, Ind. Fil. 398 (1906).

Similar to the preceding species, but pinnules small, not over 9 mm long and 2.5 mm wide, obtuse.

Rhizome short-creeping, ca. 1 mm in diam.; scales small, yellowish-brown, lanceolate, acuminate, up to 0.7 mm long, 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* rather close, 2–9 cm long, from $^1/_5$ the length of to about as long as the lamina, ca. 0.5 (0.4–0.6) mm in diam. near the apex, stramineous or pale reddish-brown, rather shining, especially at the dark base, quadrangular (at the apex sharply, otherwise obtusely), or the adaxial side angular at the apex only, for the rest, as the abaxial side, terete or subterete. *Lamina* once or twice pinnate, thinly herbaceous, medium green, 8–16 cm long, when bipinnate with 1–4 pinnae to a side and a conform terminal one. *Primary rachis* of bipinnate leaves adaxially flattened or shallowly sulcate and angular, abaxially terete. Axillary cushions not seen. Pinnae subopposite, ascending under an angle of ca. 40°, subsessile or the terminal shortly stalked (up to 5 mm), ca. ¾–1 cm apart, ca. 6–7 cm long, 7–18 mm wide, the terminal mostly longest, widest just above the base, gradually narrowed in the upper half or two-thirds, slightly narrowed at the base. Secondary rachises adaxially flattened and angular or sulcate, abaxially similar but with a terete basal portion of up to 1 cm; rachis of simply pinnate leaves similar but not terete at the base. *Pinnules* ca. 25–60 to a side, subopposite or alternate, close but hardly or not contiguous, short-stalked (up to 1 mm), spreading, but because of the convex lower margin seemingly ascending, the largest 5–9 mm long, 2–2.5 mm wide, mostly 3–3½ × as long as wide, lanceolate, almost crescent-shaped, a few lower ones usually somewhat shortened and deflexed, a strongly reduced axillary pinnule present in bipinnate leaves. Inner margin slightly convex, parallel to the rachis or divergent, lower base cuneate, in the larger pinnules stalk-like, upper base angular or subauriculate, lower margin evenly convex, upper margin concave, usually somewhat constricted near the middle, subentire or often erose-repand, not rarely somewhat undulate-crispate, apex very obtuse, pointing obliquely upwards. Marginal thickening very inconspicuous except at the base of the lower margin. Veins immersed, obscure, rather irregular, simple or the basal ones once, rarely twice, forked, ½–1 mm apart at the margin, the main vein ca. 0.2 mm above the lower margin. Upper pinnules gradually and strongly reduced, confluent (4–10 connected by a wing), the uppermost ca. 2 mm long, terminal segment lanceolate-linear, lobed-repand, obtuse, sterile or soriferous in the basal lobes, 5–15 mm long. *Sori* continuous along the upper margin, often not quite reaching the apex; indusium pale, greyish or brownish, subentire, 0.15–0.25 mm wide, not reaching the margin by a distance of 0.10–0.15 mm, reflexed or not at full maturity. Sporangia ca. 145 × 100 μ; annulus with 9–14 indurated cells; spores trilete, very pale brown, ca. 24 μ.

Distribution: Only known from the type-collection. No ecological data extant.

PERÚ. SAN MARTÍN: Mt. Guayrapurima near Tarapoto, Spruce 4023 (B, HOLOTYPE; Isotypes in BM, BR, C. Chr. in BM, F, G, K, LE, W).

It is doubtful whether this is more than a very small, perhaps depauperate, form of *L. arcuata*. There are a few small specimens of that species, e.g. Stübel 904 from Ecuador (B) and Lehmann XXXIII from Colombia (B), which approach it rather closely.

Christensen re-named *L. spruceana* because its name was supposed to be a homonym of *L. sprucei* Hooker (which is *L. meifolia*); but Art. 75 (examples) of the Code of Nomenclature states explicitly that such names are not be regarded as homonyms, and Christensen's name is therefore superfluous.

18. **Lindsaea coarctata** Kramer, spec. nov. **Fig. 57**

Folia bipinnata, petiolo stramineo vel rubro-fusco, facie adaxiali angulari, plerumque etiam canaliculata, abaxiali superne adaxiali simili, inferne subtereti vel tereti; lamina herbacea, atrovirens; pinnulis anguste lanceolatis, longitudine latitudinem quinquies vel ultra sexies superante; soris continuis, indusio angustissimo, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Schultes & Cabrera 15308 from Rio Pacoa, Vaupés, Colombia (US).

Rhizome creeping, ca. 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2.2 mm long and 0.4 mm wide, with up to 10 rows of cells at the base. *Petioles* close, ca. 15–45 cm long, about as long as to 1½ × as long as the lamina, 1–2 mm in diam. near the apex, dull or ± shining, adaxially with stramineous, in the upper part more or less wing-like angles. *Lamina* ca. 15–30 cm long, dark to blackish green on the ventral, paler on the dorsal surface, with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* stramineous to reddish brown, the angles, especially on the abaxial side, pale, wing-like; axillary cushions visible as faint swellings or obsolete. *Pinnae* subopposite or alternate, or the terminal short-stalked (–1.5 cm), subsessile, spreading under an angle of 45–60°, ca. 15–20 cm long, 4–8 cm wide, suddenly narrowed at the base and at the apex. Secondary rachises abaxially terete at the base, from the level of about the second pinnule sulcate, the groove starting rather suddenly, adaxially shallowly grooved, the margins hardly wing-like. *Pinnules* ca. 15–25 to a side, alternate or the lower ones subopposite, subsessile, spreading or slightly deflexed, as far apart as they are wide or subcontiguous at their bases, 2–5 cm long, 4–8 mm wide, a few lower ones shortened, a cuneate-flabellate axillary pinnule present. Inner margin of pinnules straight, divergent, upper base slightly auricled or angular, the greatest width of the pinnules there, the outer part gradually narrowed, lower base shortly cuneate, lower margin concave throughout or convex towards the apex, upper margin convex, or concave at the apex, the pinnules then gracefully S-shaped; apex blunt or mostly long acuminate and acute, pointing outwards, obliquely downwards or—in the upper pinnules—upwards; no separate outer margin present. All margins entire in fertile pinnules, the upper margin sometimes indistinctly crispate, in sterile pinnules shallowly but distinctly (up to ½ mm) sinuate or crenate; marginal strand stramineous, inconspicuous. Veins immersed or slightly raised at their bases, the basal ones twice, the outer ones once forked, very oblique, the ends ca. 1 mm apart; main vein intramarginal, about ½ mm above the lower margin near the apex. A few upper pinnules suddenly shortened, ca. ½–1 cm long; terminal segment mostly connected by a narrow wing with the uppermost lateral pinnule, hastate, sometimes caudate at apex, 1–4 cm long, with two or rarely more large unequal basal lobes, the rest sinuate to the blunt apex, often more strongly on one side and then distinctly asymmetrical, sterile or with short sori at the base. *Sori* along the upper margin, sometimes not reaching the apex; indusium greyish- or brownish-green, 0.1–0.2 mm wide, not reaching the margin by a distance equal to once or twice its width, reflexed and conceiled at full maturity. Sporangia ca. 142 × 95 μ; annulus with 8–11 indurated cells; spores very pale brownish, ca. 18–21 μ.

Distribution: Western Guayana and south-eastern Brazil; one of the few species with a strongly discontinuous area (map 23). Reported to be terrestrial, prob. in forest, at 300 m; hardly any ecological data extant.

COLOMBIA. VAUPÉS: Río Pacoa, R. Apaporis-trib., 0°20′ N., 71°20′ W., Schultes & Cabrera 15308 (US, HOLOTYPE); R. Piraparaná, R. Apaporis-trib., headwaters of Caño Tumuña, Schultes & Cabrera 17371 (US).

BRAZIL. AMAZONAS: Panuré, R. Uaupés, Spruce 2673 (K; fragm. in B).

RIO DE JANEIRO: Corcovado, Serra d'Estrella, Martius s.n. (M; also bearing the loc. "Japura").

SÃO PAULO: Mt. Arassojava, Martius s.n. (M). Without exact loc., "prov. Paraënsis et Rio Negro, variis locis", Martius s.n. (M; atypical, appr. *L. surinamensis*).

The name *L. coractata* was published by Kunze (Bot. Zeit. 8:326, 1850) for one of the Brazilian specimens, but with hardly any description, and must be considered as a *nomen nudum*.

A remarkable species, most closely related to *L. surinamensis* (where see for the differences), also to *L. arcuata*, which has less elongate and less acuminate pinnules, a different terminal segment, and is not rarely simply pinnate. *L. hemiglossa* is perhaps a more distant relative.

19. **Lindsaea surinamensis** Posthumus, Rec. trav. bot. néerl. 23:401 (1927), fig. 1; Fl. Surin. Suppl. 72 (1928); Alston, Kew Bull. 1932:311. **Fig. 58**

Type: Boschwezen (B.W.; Stahel & Gonggrijp) 641 from Brownsberg, Suriname (U!).

Misapplied names: *L. trapeziformis* of Baker, Fl. Bras. I²:355 (1870), p.p. min., excl. synon.

L. arcuata auct. non Kunze; Jenman, W. Ind. Gui. F. 74 (1899).

Petioles pale to reddish brown, abaxially terete below, angular above; lamina usually simply pinnate, herbaceous; pinnules lanceolate, ca. 5 × as long as wide, acuminate, the apex obtuse or subacute; upper pinnules somewhat reduced; sori continuous; spores trilete.

Rhizome creeping, 1–2 mm in diam.; scales narrowly lanceolate, very dark brown, up to almost 1 mm long and 0.2 mm wide, with 4–5 rows of cells at the base. *Petioles* close, subdistichous, 5–10 (–20) cm long about half as long as the lamina, ½–¾ mm in diam. at the apex, rather dull, adaxially flattened and bordered by paler margins almost throughout, abaxially angular above, the angles of both sides more or less wing-like. *Lamina* simply pinnate (very rarely bipinnate, with one pair of primary pinnae ca. 12 cm long), 11–20 cm long, 3–5 cm wide, pale to medium green. *Primary rachis* similar to the upper part of the petiole, surfaces flat to channelled (sec. rachises similar, abaxially terete at the extreme base). *Pinnules* 11–21 to a side, slightly falcate, subopposite to alternate, spreading, sessile, 1.5–2.5 cm long, 3.5–5 mm wide, widest at base, thence gradually narrowed to the acute or shortly acuminate apex. Inner margin straight, divergent, meeting the upper margin under an open angle, or the upper base shortly rounded, upper margin rather evenly and feebly convex, or straight to shallowly concave at base, lower margin shallowly concave, no outer margin developed. Margins entire, or in sterile pinnules with a few shallow crenations towards the apex, inconspicuously thickened. Veins slightly elevated on the dorsal surface, at least near the base, otherwise immersed, once or twice forked, not close, ca. 1 mm apart at the margin; main vein ca. 0.4 mm above the margin. Upper pinnules not strongly reduced, ca. ½–1 cm long, mostly one of them connected by a narrow wing with the terminal segment, which is subsessile, 2.5–5 cm long, ca. 1.5 cm wide, lanceolate, with two short unequal basal lobes, the apex caudate, obtuse, with a median almost percurrent main vein, often soriferous at the sides. *Sori* along the upper margin; indusium 0.2–0.3 mm wide, pale greenish-brown, rather rigid, entire or slightly sinuous, ca. ⅔ cm from the margin, bulging to reflexed at full maturity. Sporangia 140 148 × 100–110 μ; annulus with 9–11, mostly 10, indurated cells; spores pale brownish-yellow, 25–28 μ, 32?

Distribution: Northern South America (map 20). Terrestrial in forests and clearings, from sea-level to ca. 300 m.

COLOMBIA. AMAZONAS–VAUPÉS: Sorotama, Río Apaporis above mouth of R. Kananarí, Schultes & Cabrera 15972 in part (US).
BRITISH GUIANA: Moraballi Creek near Bartica, Richards 154 (BM, K); Pacatout below the Kaieteur, Jenman 1384 (K); ibid., Im Thurn s.n. (K); without loc., Appun 729 (K, partly bipinnate); Rawson W. Rawson 3310 (BM).
SURINAME: Brownsberg, in forest, Boschwezen (B.W.; Stahel & Gonggrijp) 641 (U, HOLOTYPE; fragm. in US).
FRENCH GUIANA: without loc., Leprieur 159 in part (P, fragm.); Leprieur s.n. (B).

Posthumus compared this species with *L. lancea* var. *falcata* (*L. falcata*); the shape of the pinnules is, however, more like var. *leprieurii*. It is not likely that *L. lancea* is at all closely allied. The closest relative seems to be *L. coarctata*, which differs by always bipinnate leaves and by more acuminate and more strongly curved pinnules. *L. dubia* is probably also allied.

20. **Lindsaea dubia** Sprengel, Syst. Veget. IV: 79 (1827); Presl, Tent. Pterid. 131 (1836); Kunze, Anal. 38 (1837), pl. 26; Klotzsch, Linnaea 18: 544 (1844); Hooker, Spec. Fil. I: 209 (1844), pl. 64 C; Kunze, Linnaea 21: 226 (1848); Bot. Zeit. 8: 326 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 105; J. Smith, Hist. Fil, 268 (1875); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 73 (1899); Wright, Trans. Linn. Soc. Bot. II (6): 80 (1901); Diels, N. Pfl. I^4: 220 (1902), fig. 119 D, E; Bonaparte, Notes Ptérid. VII: 374 (1918); Knuth, Fedde Rep. Beih. 43 (1): 31 (1926); Posthumus, Fl. Surin. Suppl. 70 (1928); C. Christensen, Dansk Bot. Ark. 6 (3): 97 (1929); Sampaio, Arch. Mus. Nac. Rio de Jan. 32: 34 (1930); Alston, Kew Bull. 1932: 311; Posthumus, Rec. trav. bot. néerl. 31: 469 (1934); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75: 73 (1948). **Fig. 61**

Type: Richard s.n., locality unknown (prob. P, not seen; Isotype in C!).
Homotypic synonym: *L. tenera* Kaulfuss, Enum. 219 (1824), non Dryander, 1797.

Prob. homotypic synonym: *Wibelia pectinalis* Fée, Gen. Fil. 331 (1852) (*L. dubia* cited as synonym).

Petioles olivaceous to reddish brown, for the greater part quadrangular; lamina simply pinnate, herbaceous to chartaceous; pinnules linear, 10– over 20 × as long as wide, the outer part of the upper margin in fertile pinnules mostly crenate, in sterile ones crenate throughout; upper pinnules somewhat reduced; terminal segment usually asymmetrical; sori continuous or at the apex mostly strongly interrupted; spores trilete.

Rhizome short-creeping, ca. 3/4–1 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long, 0.15 mm wide, with up to 5 rows of cells at the base. *Petioles* close, 3.5–14 cm long, about half as long to as long as the lamina, 0.5–0.7 mm in diam. near the apex, mostly dull, the upper part quadrangular with paler angles and flat or shallowly concave surfaces, the angles gradually evanescing downwards, those of the abaxial side in the lower third or fourth, the adaxial ones just above the base. *Lamina* ovate-lanceolate, 7–17(–25) cm long, 4–8 cm wide, dull, dark bluish-green on the ventral, paler on the dorsal surface, of almost equal width throughout, shortly narrowed at the apex, sometimes also at the base when the lower pinnules are deflexed, with 8–40, mostly 12–25 pinnules to a side. *Rachis* similar to the upper part of the petiole. *Pinnules* opposite or subopposite, the upper ones mostly alternate, spreading or the lower ones deflexed, sometimes upcurved in the outer part, 3–5 mm apart or the basal ones more remote, 15–40 mm long, 1–2 mm wide, windest just above the long-cuneate, not rarely somewhat stalk-like base, thence gradually tapering to the obtuse apex, sometimes slightly decurved at the base. Lower margin entire, upper margin in fertile pinnules entire at the base, the outer part crenate, with acute incisions 0.3–0.5 mm deep, the teeth between them rounded, oblique uninerval; in sterile pinnules the whole upper margin with such incisions. Rarely, small fertile pinnules are quite entire. In large, wide pinnules with upcurved apex there is sometimes a separate outer margin at the lower side of the appical part of the pinnule, often with a few teeth, and a more or less median main vein. Inner margin obliquely divergent, meeting the upper margin under an open angle. Marginal thickening very weak, not discoloured. Veins, especially the distinctly intramarginal main vein (0.3–0.4 mm from the lower edge) somewhat elevated near their bases, otherwise immersed, lateral veins very oblique, lax, springing from the main vein at intervals of 2–3 mm, simple, or the basal ones mostly forked just below the receptacle. One to four upper pinnules somewhat shortened, in addition mostly one or two at a side strongly upcurved and connected by a wing with the terminal segment, which is usually curved to the side of the uppermost confluent lateral pinnule, on the convex side entire or crenate at the base only, on the concave side crenate throughout, in size comparable to the lateral pinnules or a little shorter, sterile, or soriferous in a few of the basal teeth. Aberrant forms are not very rare, e.g. symmetrical terminal segments, or two, facing each other with the convex entire side. *Sori* continuous in the basal part of the upper margin, occupying 3–6 (or, as they are mostly forked below the receptacle 6–12) veins, short and uninerval in the lobes of the outer part, the outermost lobes mostly sterile, rarely the whole upper margin occupied by one continuous sorus; receptacle of uninerval sori considerably longer than the width of a vein-end, ca. 1–2 mm long. Indusium attached at the base only, 0.2 mm wide, entire, almost reaching the margin, somewhat reflexed at full maturity. Sporangia ca. 135 × 115 μ; annulus with 9–13 indurated cells; spores pale brownish-yellow, ca. 22–27 μ.

Distribution: Northern South America (map 19). In forests, terrestrial, on clay banks, and in crevices of rocks, sometimes in clearings of ravines, once reported as epiphytic on a palm (*Attalea*), from sea-level to ca. 1000 m. According to Jenman common in forests near river-banks in Br. Guiana.

COLOMBIA. VAUPÉS: Cerro de Circasia, Cuatrecasas 7189 (GH, US).

AMAZONAS–VAUPÉS: Sorotama, Río Apaporis, Schultes & Cabrera 15972 in part (US), 15975 (US); R. Apaporis, between R. Pacoa and R. Kananarí, Schultes & Cabrera 13002 (US).

SANTANDER: Magdalena valley, near Barranca Bermeja, Haught 1369 (GH, UC, US; atypical, with short, strongly upcurved pinnules, sori mostly quite continuous, also on the outer margin).

VENEZUELA. AMAZONAS: Capihuara, Upper Casiquiare, on palm trunks, Ll. Williams 15818 (US); w. foothills of Serra Imeri, near Salto de Huá, Holt & Blake 491 (NY, US).

BOLÍVAR: Rapids of Río Apácara, w. side of Apácara-tepuí, Chimantá-Massif, Steyermark 74684 (US); ibid., n.-w. part of Abácapa-tepuí, Steyermark 74827 (US); Mt. Roraima, Venezuelan side, Schomburgk s.n. (K).

BRAZIL. AMAZONAS: Near Panuré, Rio Uaupés, Spruce 2599 (B, BM, C, F, G, GH, GOET, K, L, LE, US, W); Rio Uaupés, Taracuá, Igarapé da Chuva, Schultes & Pires 9068 (US); Taracuá, Roman 13 (C. Chr. in BM, S–PA).
BRITISH GUIANA: Moraballi Creek near Bartica, Essequibo R., Sandwith 114 (K); ibid., Richards 148 (BM, K); Mazaruni R., McConnell & Quelch 593 (K); ibid., Appun s.n. (K); Appun 57 (B, W); ibid., Kurupung, Lang 310 (NY); Amutu, Potaro R., Im Thurn s.n. (K); Pacatout, below the Kaieteur, Jenman 1383 (K); Yamakuri, Berbice-Rupununi Cattle Trail, Abraham 225 (NY, US); Macouria Creek, Jenman 2273 (BM, US), s.n. (NY, very large form); Mt. Roraima, Schomburgk 47 in part (B, BM, US); without loc., Lobscheid s.n. (W); Schomburgk 145 (BM, K), 256 (B, BM, K), 1134 (B).
SURINAME: Brownsberg, Boschwezen 3194 (U); ibid., Stahel & Gonggrijp 327 (U, US); Nassau Mts., Lanjouw & Lindeman 2224 (U); Upper Wayombo R., Gonggrijp & Stahel 1095 (Pic.-Ser., U); Suriname R. near Morningstar Creek, Went 509 (U); Wilhelmina Mts., Stahel 484 (U); Saramacca R. headwaters, Maguire 24136 (A, NY, U, US); Tafelberg, Maguire 24345a (NY, U, US); ibid., East Ridge Creek, Maguire 24531 (A, F, K, NY, U, US).
FRENCH GUIANA: "Cayenne", Rawson W. Rawson 2309 (BM); Mt. Oyor, Leprieur 38 (B, C, C. Chr. in BM, GH, K, LE, P, US); 158 (FI, G); s.n. (F); Acarouany, Sagot 949 (B, BM, G, GH, GOET, K, NY, U, W); ibid., Kappler 1757 (B, G, GOET, L, MO, W); Conana & Inini, Richard s.n. (P, perhaps Isotype); without loc., Jelski 33 (LE); Leprieur s.n. (K); Poiteau s.n. (K); Perrottet s.n. (G).
Without any loc., Richard s.n. (French Guiana?) (C, Isotype).

A very clear-cut and outstanding species, unlike any other neotropical species. The linear pinnules, with the upper margin entire at the base, with continuous sori, crenate towards the apex, with short interrupted sori, are very characteristic. The only species somewhat comparable to *L. dubia* known to the author is *L. sinuato-crenata* v.A.v.R. from New Guinea, which, however, belongs to a quite different group, having a downwards gradually reduced lamina and somewhat anastomosing veins.

21. **Lindsaea herminieri** Fée, 11ᵉ mém. 15 (1886), t. 6 fig. 1 (as *L'Herminieri*); Duss, Fl. Crypt. Ant. franç. 59 (1904); Domin, Pterid. Domin. 245 (1929); Stehlé, Caribb. For. 4 (2): 92 (1943); not of Posthumus, Fl. Surin. Suppl. 73 (1928). **Fig. 59, 60**

Type: L'Herminier s.n. from Guadeloupe (P!).
Homotypic synonym: *L. trapeziformis* Dryand. var. *L'Herminieri* (Fée) Kuhn ex Krug apud Urban, Engl. Bot. Jb. 24: 91 (1897).

Petioles stramineous, quadrangular; lamina bipinnate with conform terminal pinna, rarely simply pinnate, thinly herbaceous; pinnules ± rhombic, with a more or less protracted apex, 2½–3½ × as long as wide, the upper ones hardly or not reduced; terminal segment slightly connected or free; sori continuous but often interrupted at the protracted apex; spores trilete.

Rhizome creeping, 2–2.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.2 mm long, 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* rather close to close, 20–27 cm long (in simply pinnate leaves ca. 10–20), about as long as the lamina, 1–1.3 mm in diam. near the apex, rather dull, adaxially for the greater part sulcate, abaxially mostly sulcate above. *Lamina* rather pale yellowish-green, especially on the dorsal side, 18–40 (in simply pinnate leaves 14–20) cm long, when bipinnate with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole. Axillary cushions visible as indistinct swellings or obsolete. *Pinnae* subopposite or alternate, 2.5–6(–9) cm apart, laxly spreading under an angle of ca. 60°, short-stalked or mostly sessile, the terminal with a stalk of up to 3 cm, 10–25 cm long, 2.5–5(–7) cm wide, hardly or not narrowed at the base, very slightly narrowed above, abruptly narrowed in the terminal segment. *Secondary rachises* adaxially narrowly and deeply sulcate, abaxially terete at the extreme base, from the level of the first to third pinnule angular, the angles mostly sharp, not or hardly discoloured, not wing-like, the surface between them flattened or shallowly concave; rachis of terminal pinna and of simply pinnate leaves angular throughout. *Pinnules* ca. 10–30 to a side, alternate or the lower ones subopposite, laxly to strongly ascending, sessile, roughly rhombic, with a protracted apex which is rudimentary or up to 2 cm long, 20–35 mm long (measured along the lower margin), 7–12 mm wide. Inner margin straight, at least in the lower pinnules divergent from the rachis, upper base angular, lower base cuneate, not stalk-like, upper margin straight or mostly concave, the bottom of the concavity near the middle of the pinnule, occasionally lobed, lower margin straight or often shallowly concave, outer margin straight or somewhat concave, the protracted apex obtuse or subacute. Upper and outer margin shallowly to distinctly sinuate in fertile pinnules, shallowly to distinctly crenate in sterile ones (which are quite common); marginal thickening indistinct except along the lower margin. Veins immersed, the inner ones once or twice forked, the outer ones simple, their ends 1–1.5 mm apart; at least the outer ⅔ of the pinnule with a slightly flexuose diagonal main vein. Upper pinnules often with upcurved apices. Terminal segment connected with a very narrow wing with the uppermost pinnule or practically free, large, broadly lanceolate, hastate, with several narrow mostly acuminate lobes at the base, the central shank sinuate to crenate, often caudate, the base cuneate, with concave sides, 2.5–5 cm long, sterile or soriferous in the lower lobes. *Sori* along the upper and outer margin; indusium pale, yellowish, entire, ca. 0.2 mm wide, about equally far to twice as far from the margin, somewhat reflexed at full maturity. Sporangia ca. 145 × 120 μ; annulus with 10–12 indurated cells; spores very pale, ca. 23–30 μ, 16?

Distribution: Endemic in Guadeloupe. In forests, ca. 250–500 m.

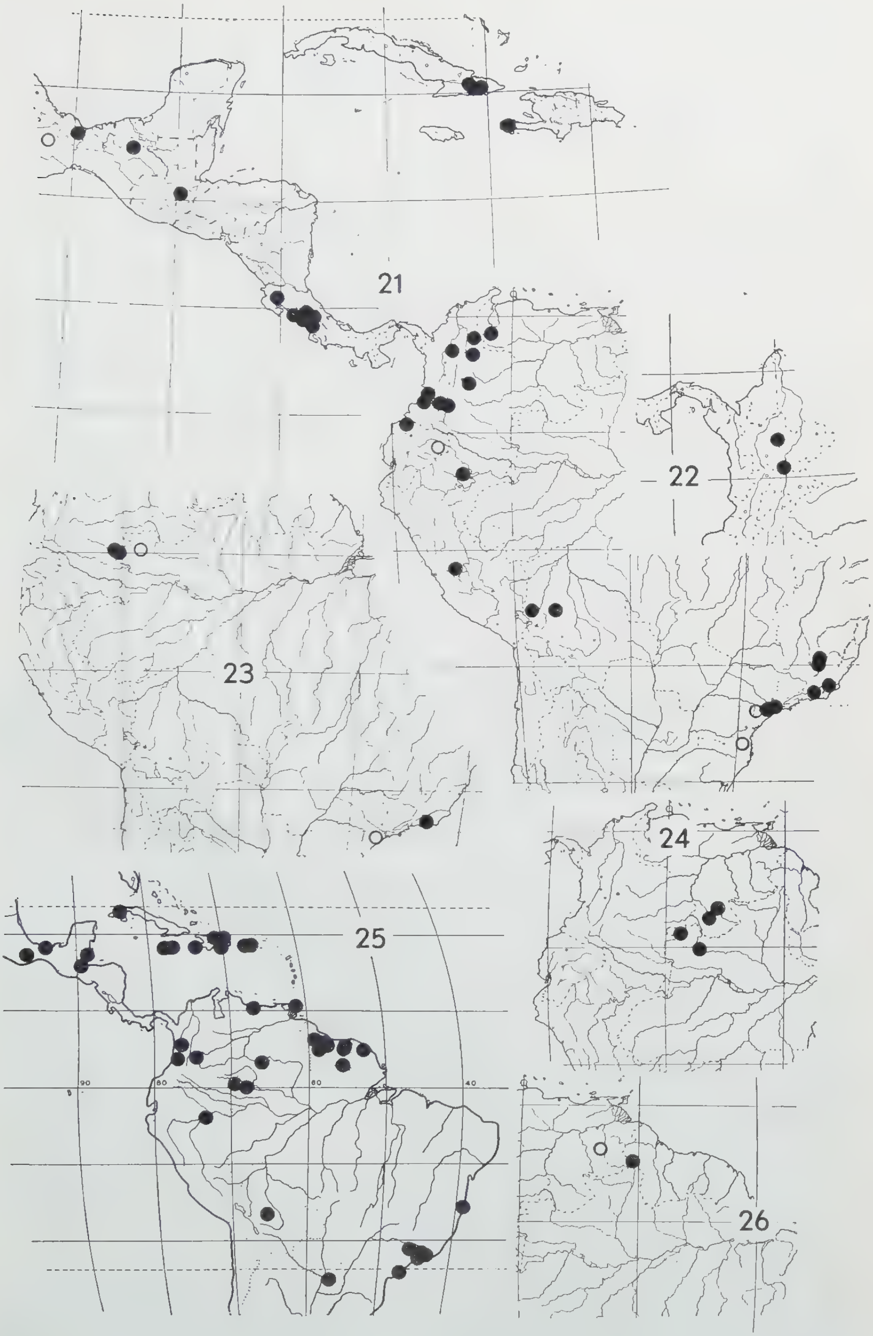
GUADELOUPE: L'Herminier 2 (B), 43 (B, G, K, W), s.n. (P, HOLOTYPE, 2 sh.; Isotypes in BM, C. Chr. in BM, F, G, L, NY); Duss 4237 (NY, US), s.n. (F, NY, US); Questel 2631 (US); Mazé 737 (K); Husnot 273 (BM).

In spite of the variable shape of the pinnules this is a very distinctive species, marked by ascending rhombic, ± caudate pinnules and large, almost free terminal segment. Posthumus included in this species two specimens from Suriname which have somewhat similar pinnules but differ in the non-divergent inner margins, spreading, less constantly caudate pinnules, and smaller, more highly connected terminal segment; they are referred with misgivings to the caudate form of *L. arcuata*. The closest relative of *L. herminieri* is probably *L. quadrangularis* ssp. *antillensis*.

Fée and most subsequent authors spelled the name "L'Herminieri", which stands for "Le Herminieri" and is contrary to Art. 23 of the Code. As it would not be a very desirable solution to hyphenate or unite the two words ("le-herminieri" or "l-herminieri" or "lehermi-nieri" or "lherminieri"), the name is spelled here "herminieri" (a spelling already adopted by Duss, l.c.), although this change affects the first letter. This spelling is in agreeance with such names as *Elaphoglossum herminieri* and the genus *Herminiera* (= *Aeschynomene*, *Papilionaceae*).

22. **Lindsaea taeniata** Kramer, spec. nov. **Fig. 62**

Folia bipinnata, petiolo stramineo vel pallide fusco, facie abaxiali obscure angulari vel subtereti; lamina herbacea, laetevirens, pinnulis



Map 21: *L. arcuata*. Map 22: *L. taeniata*. Map 23: *L. coarctata*. Map 24: *L. hemiptera*. Map 25: *L. portoricensis*. Map 26: *L. tenuis*.

anguste lanceolatis, longitudine latitudinem 5 usque ad 7½ × superante, basi solo dimidiatis, medio at apice marginibus ambobus fertilibus, apice adscendente, obtuso vel aubacuto, vena mediali flexuosa munito; soris continuis, indusio integro, marginem non attingente; sporis tetraedriformibus.

Typus: Kalbreyer 1345 from Dos Quebradas, Antioquia, Colombia (B).

Rhizome (only small pieces seen) creeping, stout, ca. 3 mm in diam.; scales lanceolate, acuminate, up to more than 2 mm long, 0.4 mm wide, with up to 11 rows of cells at the base. *Petioles* up to 50 cm long, about as long as the lamina, 1–3 mm in diam. near the apex, ± shining, adaxially strongly channelled, the channel broad and almost flat towards the apex, abaxially obtusely angular to subterete (often crushed or incompletely collected in the few specimens extant). *Lamina* ca. 25–50 cm long, with 1–2 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially sometimes shallowly sulcate in the upper part. Axillary cushions present as swellings, not discoloured, or obsolete. *Pinnae* subopposite, ascending under an angle of ca. 45°, 8–9 cm apart, stalked (the lateral 1–3.5 cm, the terminal up to 4.5 cm), ca. 17–40 cm long, (5–)9–10 cm wide, widest in the lower third, slightly narrowed at the base, rather abruptly narrowed in the upper third or fourth. Secondary rachises adaxially broadly and shallowly channelled, abaxially flattened-angular, the flattened portion passing into a channel towards the base which evanesces rather suddenly at the level of the first or second pinnule, the extreme base terete. *Pinnules* 20–30, mostly ca. 25, to a side, usually at least the lower ones subopposite, spreading or slightly ascending, sessile, separated by interstices equal to their width or half their width, the largest 3½–5 cm long, 6–7 mm wide. Inner margin straight, parallel to the sec. rachis or slightly divergent, lower base cuneate, not stalk-like, upper base ± rectangular, upper margin approximately straight in the basal part, slightly concave in the somewhat falcate-ascending apical part of the pinnule, lower margin straight or slightly concave in the basal part (1–1.5 cm), then passing under a more or less developed open angle into what is really the outer margin which is approximately straight. The greater part of the pinnule consists of the protracted apex which is soriferous at both sides, gradually narrowed, obtuse or subacute, sinuate when sterile. Marginal thickening very inconspicuous except at the extreme base of the lower margin, entire. Veins immersed, very oblique, once or twice forked, lax, their ends ca. 1 mm apart along the upper margin. Main vein diagonal from the base to the apex, flexuose in its outer part. Upper pinnules gradually reduced (strongly only in the upper third or fourth of the pinna), the uppermost ca. 4 mm long, a few connected by a very narrow wing with the terminal segment which is narrowly lanceolate, subhastate-lobed at the base, up to 3½ cm long, often caudate, obtuse, soriferous below, sterile and subentire to shallowly sinuate above. *Sori* along the upper and the greater part of the lower (really the outer) margin, absent from the extreme base of the lower margin and mostly from the outer part of the apex; indusium pale, delicate, 0.15–0.20 mm wide, its edge ca. 0.5 mm from the margin, bulging at full maturity, sometimes covered by the reflexed margin. Sporangia ca. 122 × 90 μ; annulus with 10–12 indurated cells; spores very pale, ca. 22 μ.

Distribution: Only known from the dept. of Antioquia, Colombia (map 22). In light forests and in open places in forest, 1000–2000 m.

COLOMBIA. ANTIOQUIA: Dos Quebradas, Kalbreyer 1345 (B, HOLOTYPE; Isotype in K); Amalfi, La Vivora, Kalbreyer 1650 in part (B).

A most distinctive species, outstanding by the very elongate pinnules which are dimidiate only at the extreme base and have a completely diagonal midrib. The tendency towards a protracted apex of the pinnule, found regularly in *L. herminieri*, sometimes in *L. arcuata*, and occasionally in other species, is developed here to an extreme degree;

the pinnules approach those of quite unrelated species usually segregated as *Schizoloma* whose diagnosis would include *L. taeniata*. Its closest relative is undoubtedly *L. arcuata*, the caudate form of which is very close to *L. taeniata* but differs in less elongate, closer pinnules and an always sterile non-dimidiate outer part.

23 **Lindsaea divaricata** Klotzsch, Linnaea 18:547 (1844); Kunze, Bot. Zeit. 8:349 (1850); Kuhn, Chaetopt. 26 (1882); Hieronymus, Hedwigia 62:15 (1920); not *L. divaricata* (Schlecht. & Cham.) Mett. ex Kuhn, Jo. Bot. 15:231 (1877), which is *Odontosoria schlechtendalii* (Presl) C. Chr. **Fig. 63**

Type: Schomburgk 368 from British Guiana (B!).

Heterotypic synonym: *L. trapeziformis* Dryand. var. *erythromera* Kunze, Linnaea 21:227 (1848). Type: Kegel 698 in part, from Oude Rijweg, Suriname (GOET)!.

Misapplied names: *L. trapeziformis* auct. non Dryand.; Baker, Fl. Bras. I^2:355 (1870), in part, excl. syn.; t. 21 fig. 17, prob. also fig. 16.

L. trapeziformis Dryand. var. *β arcuata* (non *L. arcuata* Kunze); Baker, Fl. Bras. I^2:355 (1870), p. p. min., excl. syn.

L. caudata auct. non Hooker; Jenman, W. Ind. Gui. F. 75 (1899)?

L. *quadrangularis* auct. non Raddi; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930).

Petioles castaneous to almost black, abaxially terete, adaxially above with pale membranous wings, similar wings on the adaxial side of the primary and on both sides of the secondary rachises; lamina bipinnate with conform terminal pinna, herbaceous: pinnules ca. 2½ × as long as wide, the upper ones reduced; terminal segment rather large, not distinct; sori continuous; indusium very narrow, entire or subentire; spores trilete.

Rhizome creeping, 2–2.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.4 mm long, 0.2 mm wide, with up to 8 rows of cells at the base. *Petioles* close, ca. 10–60 cm long, from about as long as to (in very large leaves) almost twice as long as the lamina, 1–2.5 mm in diam. near the apex, stronger at the base, shining, adaxially near the apex with a flattened portion bordered by pale membranous wings which gradually evanesce downwards, the lower half or two-thirds of the petiole quite terete. *Lamina* dark green, often brownish or blackish, on the ventral side, paler on the dorsal side, with 2–7, mostly 3–5 pinnae to a side and a conform terminal one. *Primary rachis* castaneous to reddish brown, shining, ca. 1–1.5 mm in diam., abaxially terete, adaxially with two lateral spreading pale to brownish wings 0.2–0.3 mm wide. Axillary cushions present as distinct, often discoloured swellings. Pinnae alternate or the lower ones subopposite, laxly spreading under an angle of ca. 45–60°, ca. 2–5 cm apart, subsessile or with a short stalk up to 1.3 cm long, 7–30, mostly 12–25 cm long, the upper ones somewhat shortened, the terminal about the size of the basal, (1.5–)2–4 cm wide, widest ca. $^1/_3$ from the base, thence gradually but not strongly narrowed to the base, with one or mostly several shortened pinnules to a side, a strongly reduced axillary pinnule often present, not strongly narrowed upwards to near the apex, occasionally more gradually so. Secondary rachises adaxially with similar wings as the primary rachis (fig. 6), but these narrower, occasionally almost obsolete, abaxially with similar wings which arise above the base, at the level of the first or second pinnule, and evanesce gradually in the apical part; rarely, they are absent from the entire lower half. *Pinnules* 15–30, mostly about 25, to a side, close, subcontiguous to contiguous, occasionally somewhat overlapping (succubous), spreading or, especially the upper, somewhat ascending, never decurved, 10–20(–23) mm long, 4–8 mm wide, mostly alternate throughout, in shape intermediate between those of *L. lancea* and *L. quadrangularis*, or almost matching one of them. Inner margin ± straight, parallel or somewhat divergent from the sec. rachis, lower margin straight or somewhat concave, mostly convex towards the apex; upper margin slightly convex to almost straight, very gradually passing into the more strongly convex outer margin, entire, or, especially towards the apex, faintly crenulate or erose when fertile, subentire or sinuate at the base, shallowly and bluntly crenate towards the apex in sterile pinnules; lower base shortly cuneate, hardly stalk-like; apex mostly subacute. Marginal strand present throughout, very narrow and inconspicuous, except at the lower base, stramineous. Veins immersed, or, especially adaxially, slightly elevated, mostly twice forked, ca. ½–¾ mm apart at the margin; main vein shortly united with the marginal strand, otherwise 0.1–0.2 mm above it. Uppermost pinnules 3–10 mm long, one or two connected by a narrow wing with the terminal segment which is triangular-lanceolate, acute, ca. 1–1.5 cm long, lobed at the base, serrate-crenate above, quite sterile or sometimes soriferous in the basal lobes. *Sori* along the upper and outer margin; indusium ca. 0.1–0.15 mm wide, not reaching the edge by a distance of ¾–1 mm, soon reflexed and quite conceiled at full maturity. Sporangia ca. 150 × 115 μ; annulus with 9–11 indurated cells; spores pale yellowish, ca. 23–28 μ.

Distribution: Rather widespread, largely in South America (map 27). In rainforests, mostly in very moist situations, sometimes along watercourses, up to ca. 750 m.

Representative or widely distributed specimens:

GUADELOUPE: Duss s.n. (F, PH).
GUATEMALA: Izabal, Bernoulli 861 (B); ibid., Bernoulli & Cario 338 (B).
PANAMÁ: Swamp near Almirante, n.w.-Pan., Rowlee & Stork 991 (NY, US).
COLOMBIA. VAUPÉS: Río Kuduyarí, R. Vaupés-trib., Schultes & Cabrera 17886 (US).
VENEZUELA. AMAZONAS: San Carlos, Río Negro, Ll. Williams 14685 (G, US); Yavita, id. 13998 in part (F).
BRITISH GUIANA: Rockstone, Essequibo R., Jenman s.n. (NY); Macouria Creek, Essequibo R., Jenman 2268 (BM, K, NY); ibid., Fanshawe M 325 (BM); Oreala, Corantyne R., Jenman 432 in part (M); without loc., Schomburgk 368 (B, HOLOTYPE; Isotype in BM).
SURINAME: Oude Rijweg, Kegel 698 in part (GOET, HOLOTYPE of *L. trapeziformis* var. *erythromera* Kunze).
FRENCH GUIANA: Near Saï R., Leprieur 16 (FI, GH, NY, US); without loc., Leprieur 10 (US), 15 (NY), 165 (G, P, U).
BRAZIL. AMAZONAS: Near Panuré, Rio Uaupés, Spruce 2325 in part (BR); Tunuy, Rio Içana, von Lützelburg 22405 (M); Barra, Rio Negro, Spruce 1367 (K); Trinidade, Rio Negro, Koch 2a (B).
GOIAS: Sucuriu on Rio das Femeas, von Lützelburg 1509 in part (M, NY, US).
MATTO GROSSO: Palmeiras, Lindman A 2385 (US).
SÃO PAULO: Retiro da Lagem near Cajurú, Regnell III 1469 (BR, M, S, UPS, US).
PERÚ. LORETO: Mishuyacu, near Iquitos, Klug 69 (F, NY, US), 1337 (F, NY, US); above Pongo de Manseriche, mouth of R. Santiago, Mexía 6133b (UC, US).
HUÁNUCO: Near Tingo María, Aguilar 301 in part (UC); ibid., R. M. & A. F. Tryon 5339 (U).
BOLIVIA. SANTA CRUZ: Buena Vista, Sara, Steinbach 5309 (GH, US).
PARAGUAY: Cordillera de Piribebuy, Balansa 4454 (B, BM, G, K, L, LE, S–PA, U, UPS, US); Sierra de Amambay, Hassler 10044 in part (B, W).

Although the character of the wings on the axes is not always readily observed, this species can be recognized without much difficulty by the dark axes, dark leaf-tissue which is often wrinkled with slightly elevated veins, and the broad almost always sterile terminal segment. It is closest to *L. quadrangularis* ssp. *terminalis*, from which it is sometimes difficult to distinguish in the southern part of its range (notably Paraguay); there may be some introgression of the two taxa.

It is surprising that this rather well-marked species almost fell into oblivion after it was published; it was incorrectly referred to *L. lancea* by Christensen (Ind. Fil. p. 393, 1906), and the specimens appear under this name or *L. crenata* (because of the crenate sterile parts of the upper/outer margin) in most herbaria. The only more modern author who apparently understood and recognized it was Hieronymus.

Several specimens from Guiana agree with *L. divaricata* in many characters, but the wings on the abaxial side of the secondary rachises are obsolete or weakly developed in the upper part; all are sterile or incompletely fertile. They are probably merely a depauperate or aberrant form of *L. divaricata.* Some of them were cited as *L. crenata* by Alston (Kew Bull. 1932:311) and by Maxon & Morton (in Maguire, Bull. Torr. Bot. Cl. 75:73, 1948). The specimens are:

BRITISH GUIANA: Potaro River Gorge below the Kaieteur Falls, Maguire & Fanshawe 23427 (US); Moraballi Creek near Bartica, Richards 55 (K); Essequibo R., 35 mi. s. of Rockstone, Guppy 100 (BM).
SURINAME: Tafelberg, Maguire 24325 (A, NY, U, US).

24. **Lindsaea guianensis** (Aublet) Dryander, Trans. Linn. Soc. 3:42 (1797); Roem. Arch. 2 (II):237 (1801); Swartz, Syn. Fil. 119 (1806); Willdenow, Spec. Pl. V:424 (1810); Desvaux, Prod. 313 (1827); Sprengel, Syst. Veget. IV:79 (1827); Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:216 (1844), p.p. mai.; Kunze, Linnaea 21:221 (1848); Fée, 11^e^ mém. 15 (1866); Hooker & Baker, Syn. Fil. 1^st^ ed. (1868), 2^nd^ ed. (1874) 107 in part; Fée, Crypt. vasc. Brés.I:31 (1869); Baker, Fl. Bras. I^2:354 (1870), in part, excl. syn.; J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), in part; Christ, Farnkr. d. E. 293 (1897); Duss, Fl. Crypt. Ant. franç. 58 (1904); Posthumus, Fl. Surin. Suppl. 73 (1928), in part; Alston, Kew Bull. 1932; 311; not of Lindman, Ark. f. Bot. 1:199 (1903), nor of Graham, Ann. Carnegie Mus. 22:87 (1934).

Basionym: *Adiantum guianense* Aublet, Hist. Pl. Guian. 2:963, 4, pl. 365 (1775); Lamarck, Encycl. I:43 (1783); J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:413 (1793).

Type: Aublet s.n. from French Guiana (P? not seen).

Heterotypic synonym: *L. guianensis* (Aubl.) Dryand. var. *imbricata* Jenman, W. Ind. Gui. F. 76 (1899). Type: Jenman s.n. (?) from Bartica Grove, British Guiana (not seen).

Misapplied names: *L. trapeziformis* auct. non Dryand.; Baker, Fl. Bras. I^2:355 (1870), p.p. min.

L. horizontalis auct. non Hooker; Shimek, Ferns Nicar. 152 (1897), pl. XI fig. 8–11.

Petioles and primary rachises of bipinnate leaves abaxially terete; lamina mostly bipinnate with conform terminal pinna, herbaceous; secondary rachises abaxially terete in the lower part; pinnules close, the upper ones gradually reduced; sori continuous; indusium narrow; spores trilete.

Rhizome creeping, prob. short; scales narrowly lanceolate, with up to 7 rows of cells at the base. *Petioles* close, very variable in length, ca. 10– over 60 cm long, from about half as long as to somewhat longer than, rarely up to 1½ × as long as the lamina, adaxially channelled almost to the base. *Lamina* bright green, sometimes dark green, paler on the dorsal side. Primary rachis (in bipinnate leaves) similar to the upper part of the petiole. Axillary cushions present, sometimes discoloured. *Pinnae* short-stalked to subsessile, laxly spreading under an angle of 40–50°, often more ascending in paucijugate leaves; secondary rachises abaxially terete below, in the upper part gradually angular, sometimes shallowly sulcate towards the apex, rarely terete for only a short part at the base. *Pinnules* subopposite or the upper ones alternate, rarely alternate throughout, close, subsessile, a few lower ones somewhat reduced, those in the upper half or third of the pinna gradually reduced, confluent in the apex. *Sori* along the upper/outer margin; indusium entire or mostly minutely erose-denticulate, distinctly intramarginal, reflexed and conceiled at full maturity. Sporangia ca. 140 × 115 μ; annulus with 9–12 indurated cells; spores very pale yellowish-brown, ca. 18–25 μ, 32?

This species consists of two quite clear-cut subspecies which may be distinguished as follows:

a. Pinnae long-acuminate; uppermost pinnules minute, 1–2 mm long; axes usually pale; almost always bipinnate . . . . a. ssp. *guianensis*

b. Pinnae acute or shortly acuminate; uppermost pinnules not denticuliform, ca. 5 mm long; axes often reddish to dark brown; pinnate or bipinnate . . . . b. ssp. *lanceastrum*

a. ssp. **guianensis**. **Fig. 27, 65**

Rhizome 3–4 mm in diam.; scales long-acuminate, up to 1.2 mm long, 0.2 mm wide. *Petiole* dark brown to blackish at the base, for the rest stramineous, rarely castaneous, rather shining, especially at the base, 1–2(–3) mm in diam. near the apex. *Lamina* bipinnate (simply pinnate almost always in juvenile specimens only), 20–65 cm long, with 1–13, mostly about 4–7 pinnae to a side and a conform terminal one; *pinnae* subopposite to alternate, rather remote, 2–4(–7) cm apart, rarely subcontiguous, ca. 10–25 cm long, the upper pinnae of plurijugate leaves shorter, ca. 2(1½–2½) cm wide, long-acuminate. *Pinnules* ca. 50(30–70) to a side, often strongly overlapping, succubous, dimidiate-ovate, occasionally subfalcate, spreading or sometimes a little deflexed, the upper ones not rarely ascending, the largest (7–)10–12 mm long, (3–)5–7 mm wide, about twice as long as wide, relatively very constant in size and shape, widest at the base or in the whole lower half. Inner margin straight, parallel or somewhat divergent from the sec. rachis, lower base cuneate, hardly stalk-like, upper base shortly rounded, lower margin straight or faintly concave, upper margin convex, but often straight at the base, a more or less separate outer margin often present; apex obtuse or subacute. Upper and outer margin often sinuous in sterile or incompletely fertile pinnules, laxly crenate in juvenile plants, otherwise quite entire. Marginal thickening stramineous, very narrow. Veins immersed but readily visible, once or twice forked, ca. 1 mm apart at the margin. Main vein and basal lateral vein ca. ¾ from the edges. Upper pinnules very gradually reduced, the uppermost pinnules in the long-acuminate or caudate top of the pinna denticuliform, ca. 1–2 mm long, rather suddenly confluent into a lanceolate-linear, often caudate terminal segment, which is obtuse, sinuous below, entire above, 1–1½(½–2½ in extreme cases) cm long, with a flexuose midrib, almost always quite sterile. Indusium ca. 0.15 mm wide, not reaching the margin by a distance equalling 2–4 × its width.

Distribution: Mostly confined to northern South America (map 28). Incorrectly reported by Baker (Jo. Bot. 25:24, 1887) from Costa Rica

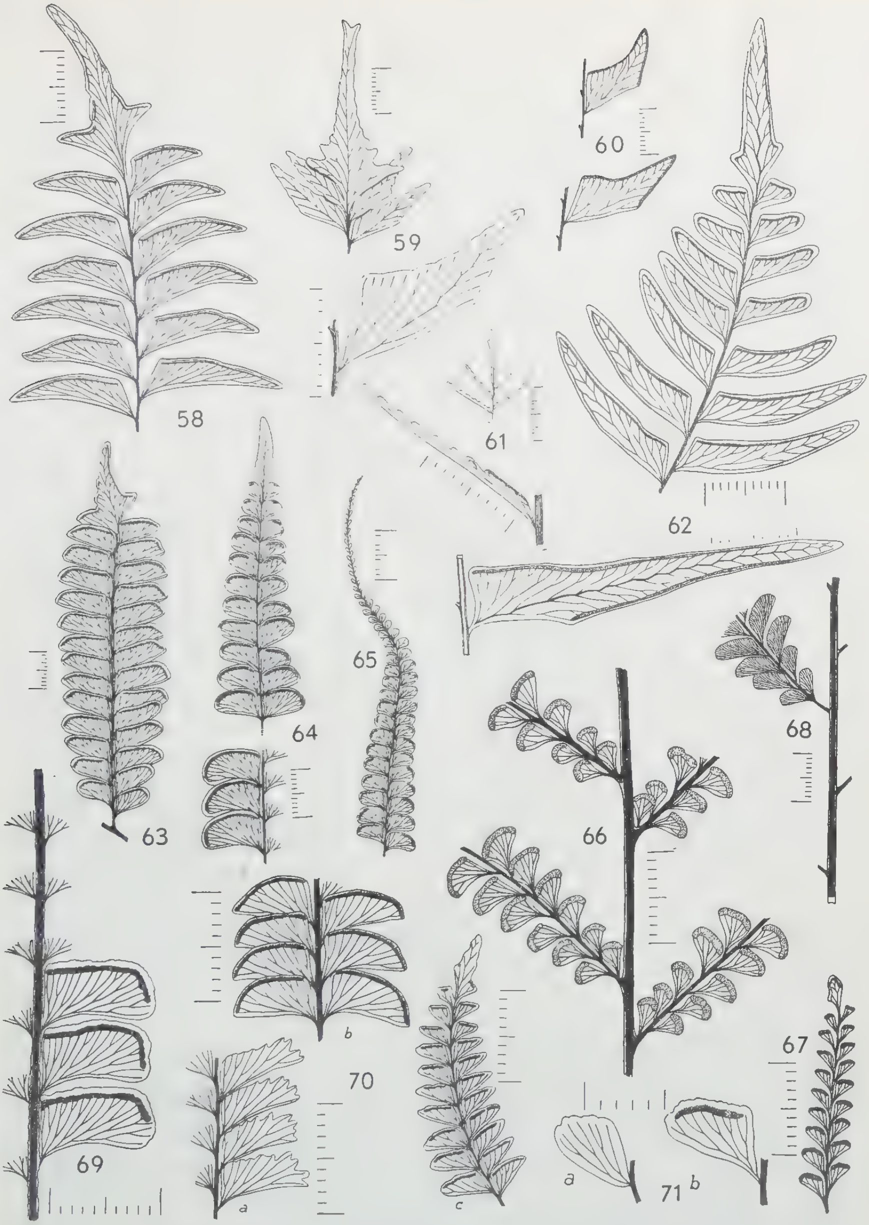


Fig. 58: *Lindsaea surinamensis;* upper half of lamina (Boschwezen 641). Fig. 59–60: *L. herminieri;* fig. 59: apex of lateral pinna (above) (L'Herminier 43), sterile pinnuel (L'Herminier s.n.); fig. 60: fertile pinnules from middle of terminal pinne (L'Herminier 2). Fig. 61: *L. dubia;* lateral pinnule (below), apex of lamina (above) (Boschwezen 3194). Fig. 62: *L. taeniata;* apex of lateral pinna (above), lower pinnule of lateral pinna (below) (Kalbreyer 1345). Fig. 63: *L. divaricata;* middle pinna (Leprieur s.n.). Fig. 64: *L. guianensis* ssp. *lanceastrum;* upper part of upper pinna (Dusén 15013). Fig. 65: *L. guianensis* ssp. *guianensis;* upper ⅔ of lateral pinna (Spruce s.n.). Fig. 66–67: *L. javitensis;* fig. 66: portion of lamina below the apex; fig. 67: apex of middle pinna (Schultes & Cabrera 14528). Fig. 68: *L. rigidiuscula;* portion of lamina (Koch 65). Fig. 69: *L. portoricensis;* base of lateral pinna (Fanshawe M 334). Fig. 70: *L. hemiptera;* a: pinnules from simply pinnate sterile lamina (Steyermark 57824); b: fertile pinnules from base of lateral pinna; c: apex of lateral pinna (Ll. Williams 15536). Fig. 71: *L. cubensis;* a: sterile pinnule, b: fertile pinnule (Wright 3947). (Scales in mm).

and by Gardner (London Jo. Bot. 1:548, 1842) from Rio de Janeiro. In forests, sometimes on tree-trunks or even pendulous from branches but mostly terrestrial, from sea-level to ca. 750 m.

Representative specimens:

Nicaragua: Camp Menocal near Greytown, Shimek s.n. (IA).
Guadeloupe: Duss 4239 in part (NY), 4139 (US), 4242 in part (NY, US); L'Herminier s.n. (B, BM, F, G, K, LE, P, US, part of Type-material of *L. montana*).
Grenada: Jenman s.n. (NY); Trinidad Bot. Gard. Herb. (Alexander 6180) (C. C. Chr. in BM, G, S-PA).
Colombia. Santander: Magdalena Valley, vic. of Barranca Bermeja, Haught 1371 (GH, UC, US); vic. of Puerto Berrio, between Carare and Magdalena Rs., Haught 1880 (GH, US); Puerto Wilches-Puerto Santos, Killip & A. C. Smith 14873 (GH, NY, S, US).
El Valle: Buenaventura, Killip 11755 (US).
Chocó: South of R. Condoto, Quebrada Guarapo-Mendinga, Killp 35142 (GH, K, UC, US).
Vaupés: R. Piraparana, trib. of R. Apaporis, Schultes & Cabrera 17399 (US).
Venezuela. Amazonas: Yavita, Ll. Williams 13998 (US); Capihuara, Upper Casiquiare, Ll. Williams 15819 (US); Maroa, R. Guainía, Ll. Williams 14277 (F).
British Guiana: Macouri Creek, Essequibo R., Jenman s.n. (NY); Kangaruma-Potaro Landing, Gleason 229 (GH, NY, US); Moraballi Creek near Bartica, Richards 30, 347, 465 (K); ibid., Fanshawe M 327 (BM); Oreala, Corantyne R., Jenman 431 (K); Berbice, Schomburgk 346 in part (BM, F, K, U, W).
Suriname: Near Blaauwe Berg, Splitgerber 888 (L); Suhoza, Upper Suriname R., Lanjouw & Lindeman 3379 (BM, U); near Jodensavanne, Kegel 1076 (GOET).
French Guiana: Acarouany, Sagot 850 (B, BM, K); Inipi, Leprieur 17 (GH, US); Mana, Perrottet s.n. (G).
Brazil. Amazonas: Panuré, Rio Uaupés, Spruce 2325 * (BM); near Manáos, Rio Negro, Ule 5419 (B, G, L); Barra, Rio Negro, Spruce 1768 (B, G); São Gabriel, Rio Negro, Spruce s.n. (B); Santarem near Pará, Spruce 349 (K).
Perú. Huánuco: Near Tingo María, Allard 21502 (US); ibid., R. M. & A. F. Tryon 5275, 5289 (U).

The most conspicuous character of this subspecies is found in the apices of the pinnae, which are long-acuminate or caudate, with a sudden transition from denticuliform pinnules to a lanceolate terminal segment.

b. ssp. **lanceastrum** Kramer, ssp. nov. **Fig. 64**

Petiolo saepe rubro-fusco vel badio, facie abaxiali petioli rhachidiumque primariarum et secundariarum tereti; lamina laete- vel atrovirens, pinnulis approximatis, saepe leviter imbricatis, semi-ovatis vel semi-ellipticis, forma *L. lanceam* imitantibus, superioribus sensim redactis, autem sine apice pinnarum longe caudato ut in subspecie guianensi; soris indusio plerumque minute eroso.

Typus: Dusén 15013 from Jaguariaiva, Paraná, Brazil (F).

Rhizome 2–3 mm in diam.; scales acuminate, up to 1¾ mm long, 0.2 mm wide. *Petioles* often rather shining, 1-1.5 mm in diam. near the apex. *Lamina* mostly bipinnate but sometimes simply pinnate in apparently full-grown plants, 20-45, mostly ca. 30–40 cm long. *Primary pinnae* (if any) 1–4(–7) to a side and a conform terminal one, subopposite or mostly alternate, rather widely spaced, (2-)3–6½ cm apart, 10- over 35 cm long, 2–4, mostly 2.5–3 cm wide, shortly narrowed at the base, gradually and strongly narrowed in the upper ⅓ or ¼; terminal pinna largest in paucijugate leaves, mostly stalked. Secondary rachises stramineous or often reddish (rarely dark) brown. *Pinnules* (15-)20–50 to a side, resembling those of *L. lancea*, spreading or somewhat ascending, the basal ones often somewhat falcate-deflexed, the largest (8–)12–20 mm long, (4.5–)5–10 mm wide, about twice as long as wide, widest at the base or of equal width almost throughout, entire. Inner margin straight, ± parallel to the sec. rachis, lower base cuneate, hardly stalk-like, upper base rounded, sometimes broadly, rarely subangular, lower margin straight or faintly concave, upper margin convex, more strongly so towards the apex, a separate outer margin mostly not present, the lower and upper/outer margin sometimes meeting at almost right angles, otherwise the apex more gradually narrowed, the very top obtuse. Marginal thickening stramineous, not prominent. Veins immersed but not obscure, mostly twice forked, their ends ca. ½–¾ mm apart; main vein shortly united with the marginal strand, ca. ½ mm above it near the apex. Upper pinnules gradually reduced, the uppermost ones ca. 5 mm long, mostly one or two connected by a wing with the terminal segment which is lanceolate, acute or obtuse, shallowly lobed to subentire, with cuneate base and a flexuose midrib, 0.5–2(–2.5) cm long, often soriferous at the base. Indusium 0.2–0.3(–0.4) mm wide, not reaching the margin by a distance equal to its width or twice as wide.

Distribution: Central, eastern, and southern Brazil; Paraguay (map 29). In swampy forests and along watercourses, up to ca. 700 m.

Representative specimens:

BRAZIL. MARANHÃO: West of Riachão, E. N. Shaw s.n. (US).

BAHIA: Pedra Santa near São Bento, von Lützelburg 18934 (M, S–PA).

GOIAS: Sucuriu, Rio das Femeas, von Lützelburg 13749a (M).

MATTO GROSSO: Santa Ana da Chapada, Buriti, Malme s.n. (Regnell II) (S); ibid., id. s.n. (Regnell II 2215a) (UPS); Floriano, Hoehne 5364 (UC).

SÃO PAULO: Campinas, Heiner 537 (S, S–PA); ibid., Severin 74 (UPS), 169 (S, UPS).

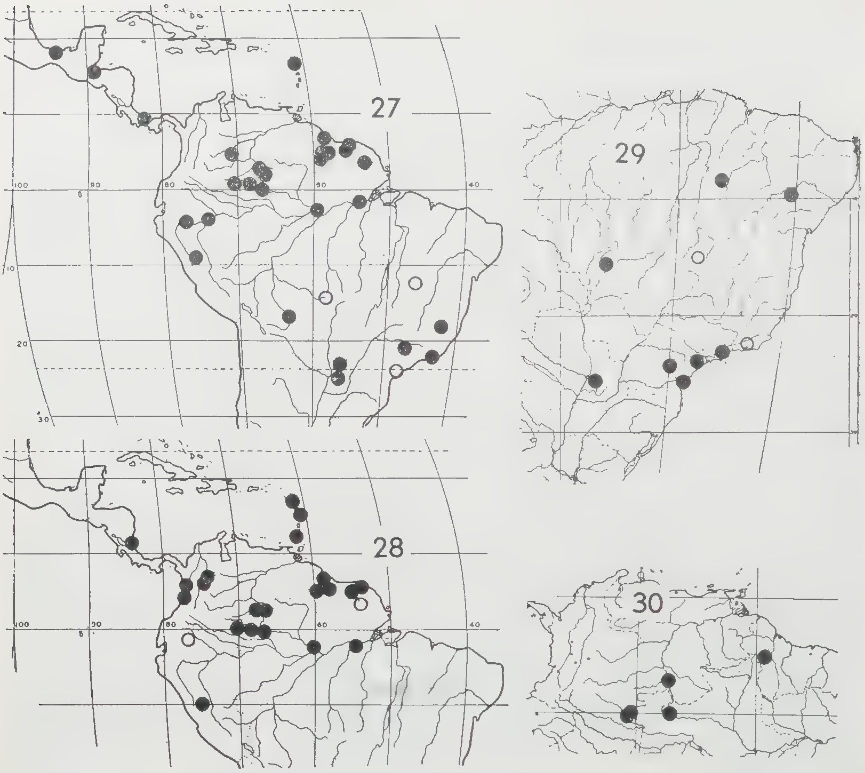
PARANÁ: Jaguariaíva, Dusén 14117 p.p. mai. (BM, G, GH, K, LE, MO, NY, S, US); ibid., id. 13213 (LE, MO, S); ibid., id. 15013 p.p. mai. (F, HOLOTYPE; Isotypes in B, BR, C, G, GH, NY, PH, S, S–PA); ibid., id. s.n. (BR, F, G, GH, MO, PH); Volta Grande, Dusén 14139 in part (B, S, S–PA); Porto Dom Pedro II, Dusén 4424 (B, BM, S); ibid., id. 9872 (BM, G, GH, K, LE, NY, S, S–PA, US).

Without loc., Riedel 17 (B, BR, C, FI, G, GH, GOET, L, LE, M, NY, S, UPS, US, W).

PARAGUAY: Paraguari, Sierra de Amambay, Hassler 10044 in part (B, K); without loc., Fiebrig 6343 in part (K, L, M).

The two subspecies, although very closely allied, are clear-cut, and there would be no fundamental objection against treating them as distinct species. The closest relative seems to be *L. quadrangularis* ssp. *terminalis*, which is quite close to *L. guianensis* ssp. *lanceastrum*, but has smaller, mostly more elongate, more remote pinnules, darker axes, esp. the secondary rachises, which are more slender, and narrower indusia. *L. hemiptera* is perhaps more distantly related.

The author has not examined the type of *Adiantum guianense* Aublet, and there is some uncertainty whether the name is correctly applied. Although Aublet's plate resembles most closely the species described above, there is a possibility that it represents a form of *L. stricta* var. *parvula*. If this would be the case, it would cause very regrettable name-changes, as *L. stricta* would have to be called *L. guianensis*, and the species which used to bear that name would need a new one. Because of this, the name *L. guianensis* is used here as currently applied. It has been widely misapplied for the lax form of *L. stricta* which is most common in south-eastern Brazil (LINDMAN, l.c., WAGNER 1952b, etc.), with which it has nothing to do, however, as this form does not occur in the Guianas.



Map 27: *L. divaricata.* Maps 28–29: *L. guianensis;* map 28: ssp. *guianensis;* map 29: ssp. *lanceastrum.* Map 30: *L. javitensis.*

Jenman's var. *imbricata* probably represents ssp. *guianensis;* the author has seen no specimen in K or NY from the forest opposite Bartica Grove, British Guiana, whence Jenman reported it, but three sheets from the Macouria Creek in NY are annotated "var. *imbricata*" and constitute at least authentic material; therefore, this name may safely be referred to ssp. *guianensis*, with which Jenman's description is in excellent agreement.

L. guianensis was chosen as type-species of the genus by Copeland (1947); for arguments against this choice, see p. 137.

25. **Lindsaea hemiptera** Kramer, spec. nov. **Fig. 70**

Misapplied name: *L. guianensis* auct. non Dryand.; Baker, Fl. Bras. I^2:354 (1870), in part, excl. syn.

Folia pinnata vel plerumque bipinnata, petiolo pullo vel atropurpureo, facie abaxiali tereti, adaxiali superne lateraliter alata; lamina rigide herbacea vel papyracea, rhachide primaria et rhachidulis secundariis parti superiori petioli similibus, pinnulis dimidiato-ellipticis, longitudine latitudinem bis vel bis et dimidius superante, pinnulis superioribus sensim decrescentibus; soris continuis, indusio rigido, angusto, integro vel subintegro, marginem non attingente; sporis tetraedriformibus.

Typus: Ll. Williams 15536 in part from Capihuara, Upper Casiquiare, Amazonas, Venezuela (US).

Rhizome short(?)creeping, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.5 mm long, 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close, ca. 8–50 cm long. about as long as the lamina, ⅔–1½ mm in diam. near the apex, shining, adaxially terete at the base, the upper ¾ or more less convex, bordered by ridges which at least in the upper half are distinctly wing-like, pale or reddish, obliquely spreading, attaining a width of ca. ¼ mm at the base of the lamina. *Lamina* medium to dark olivaceous on the ventral side, paler on the dorsal side, 15–40 cm long, with 2–6 pinnae to a side (if any) and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, the adaxial wings shortly interrupted above the insertion of the pinnae. Axillary cushions very indistinct. *Pinnae* alternate or subopposite, sessile or shortly stalked (up to 2 or 3 mm), spreading under an angle of ca. 60°, 1–8, mostly 2–4 cm apart, 10–30 cm long, 1.5–2.5 cm wide, widest in the lower third or half, slightly narrowed at the base, gradually, but not very strongly narrowed in the upper half or two-thirds. Upper pinnae slightly shortened. Secondary rachises similar to the primary, the wings shortly interrupted above the insertion of the pinnules, gradually evanescing above. *Pinnules* 35–50(–70) to a side, the lower ones mostly subopposite, the upper ones alternate, close, subcontiguous to slightly imbricate, very regularly spaced, spreading, sometimes subfalcate, ca. 9 mm long and 4 mm wide; sterile pinnules more elongate, ca. 7–10 × 3–3.5 mm, about 2½–3 × as long as wide. Inner margin straight or slightly convex, parallel or somewhat divergent from the sec. rachis, passing with a short rounded portion into the upper/outer margin which is rather evenly convex, lower margin straight or somewhat concave, lower base shortly cuneate, not stalk-like, apex obtuse or mostly subacute to acute. Fertile pinnules quite entire; sterile pinnules along the outer margin with rather irregular teeth separated by incisions 1–1.5 mm deep, often more highly united in pairs, passing rather abruptly into shallow crenations present along the upper margin; incompletely fertile pinnules with a few large teeth near the apex. Marginal thickening with a very thick stramineous or reddish portion occupying ⅓–¼ of the lower edge, there continuous with the main vein, otherwise less conspicuous but visible throughout, entire. Veins slightly elevated, especially their bases on the dorsal side, once or twice forked, close, their ends ½–⅔ mm apart; main vein 0.2–0.3 mm above the lower margin near the apex. Upper pinnules gradually reduced, more strongly so in the apical part of the pinnae which are therefore shortly acuminate; uppermost pinnules 2–5 mm long, one or a few connected by a wing with the terminal segment which is lanceolate, subacute or acute, 0.5–2 cm long, asymmetrically lobed at the base, the margin dentate-crenate, not or hardly soriferous. *Sori* along the upper/outer margin; indusium stiff, 0.2–0.25 mm wide, not reaching the margin by 0.1–0.2 mm, rarely less; sporangia ca. 150 × 115 μ; annulus with 10–14 indurated cells; spores pale brownish-yellow, ca. 23–28 μ.

Distribution: Adjacent regions of Venezuelan and Brazilian Amazonas (map 24). In moist woods, along watercourses; one record of 120 m alt.

VENEZUELA. AMAZONAS: Capihuara, Upper Casiquiare, dense forest, Ll. Williams 15536 in part (US, HOLOTYPE; Isotype in GH); between Esmeralda Savanna and base of Mt. Duida, Steyermark 57824 (F, GH, MO, NY, US).
BRAZIL. AMAZONAS: Near São Gabriel da Cachoeiras, Rio Negro, Spruce 2326 (B, K, LE); Tunuy, Rio Aiari, von Lützelburg 23658 (M, NY).

A very distinctive species, with dark, shining, abaxially quite terete, adaxially winged axes, small, evenly spaced pinnules and narrow indusia. Its alliance within the section is not quite clear; perhaps related to *L. guianensis*, or to *L. divaricata*.

26. **Lindsaea portoricensis** Desvaux, Berl. Mag. 5:326 (1811); Kuhn, Chaetopt. 26 (1882); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. mai.; Jenman, W. Ind. Gui. F. 77 (1899); Kuhn in Urban, Symb. Ant. 4:31 (1903), p.p. mai.; Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Maxon, Pterid. Port. 489 (1926); Posthumus, Fl. Surin. Suppl. 74 (1928); Domin, Pterid. Domin. 243 (1929); Weatherby, Contr. Gray. Herb. 114:26 (1936); C. Christensen, Kungl. Sv. Vet.-Akad. Handl. 16 (2):46 (1937). **Fig. 24, 69**

Type: without coll., "in Antillis", apparently from Puerto Rico (P!; the smaller part of the material belonging to *L. lancea*).

Heterotypic synonyms: *Lindsaea crenata* Klotzsch, Linnaea 18:546 (1844); Hooker, Spec. Fil. I:208 (1844); J. Smith, Hist. Fil. 268 (1875); Jenman, W. Ind. Gui. F. 73 (1899); Hieronymus, Hedwigia 62:16 (1920); Posthumus, Fl. Surin. Suppl. 74 (1928); not of most other authors. Type: Schomburgk 274 in part from British Guiana (B!).

Lindsaea rufescens (lapsu: *rubescens*) Kunze, Linnaea 21:227 (1848); J. Smith, Lond. Jo. Bot. 1:200 (1842), nomen; Kunze, Bot. Zeit. 8:385 (1850); Fée, 9^{e} mém. App. (1856). Type: Schomburgk 346 in part, from British Guiana (B!).

Lindsaea consanguinea Fée var. *β rigida* Fée, Crypt. vasc. Brés. I:30 (1869). Type; Glaziou 2805 from Jacú, Serra dos Orgãos, Rio de Janeiro, Brazil (prob. P, not seen; Isotypes in B, BR, C, K, S).

Misapplied names: *Lindsaea stricta* auct. non Dryand.; Klotzsch, Linnaea 18:546 (1844); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. min.; Kuhn in Urban, Symb. Ant. 4:31 (1903), in part.

Lindsaea guianensis auct. non Dryand.; Ettingshausen, Farnkr. t. 146 fig. 24, 25 (1865); Baker, Fl. Bras. I^{2}:354 (1870), in part, excl. of most synonyms; Posthumus, Fl. Surin. Suppl. 73 (1928), in part.

Lindsaea quadrangularis auct. non Raddi; Fée, Crypt. vasc. Brés. I:29 (1869), in part.

Lindsaea consanguinea of Fée, ibid. 30 (1869), non 11^{e} mém. 16 (1866).

Lindsaea trapeziformis auct. non Dryand.; Baker, Fl. Bras. I^{2}:355 (1870), p.p. min., excl. syn.

Petioles brownish red or dark brown, abaxially terete; lamina simply pinnate or bipinnate with conform terminal pinna, firmly herbaceous to chartaceous; secondary rachises abaxially with paler angles which are irregularly interrupted at the base; pinnules subrectangular or mostly tongue-shaped, ca. 2 × as long as wide; veins often visible as wrinkles in the leaf-tissue; upper pinnules gradually reduced; sori continuous; indusium mostly repand-erose; spores trilete.

Rhizome creeping, ca. 1½–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1¾ mm long and 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* ± close, ca. 5–50 cm long, ratio to length of lamina very variable, ¾–2 mm in diam. near the apex, dull or often shining, adaxially mostly terete below, rarely for the greater part or at the extreme base only, flattened above, with sharp, sometimes paler but never wing-like borders, abaxially terete, or rarely with short lateral angles near the apex. *Lamina* on the ventral side medium or mostly dark olivaceous to brownish-green, on the dorsal side similar or somewhat paler, quite dull, ca. 15–50 cm long, when simply pinnate considerably longer than the petiole, up to six times as long, when bipinnate of comparable size, often not more than two-thirds the length of the petiole, with one odd pinna at one side to 4(–6) on each side and a conform terminal one. *Primary rachis* of bipinnate leaves similar to the upper part of the petiole, abaxially often flattened and laterally angular above, rarely throughout; of simply pinnate leaves as the secondary rachises of bipinnate leaves. Axillary cushions often visible as swellings, not discoloured. *Pinnae* strongly ascending, often almost vertical, touching each other and the terminal pinna, the lower ones 3–5 cm apart, the upper ones gradually closer in plurijugate leaves, subsessile, the terminal mostly stalked (up to 3 cm), the lower ca. 15–25(–40) cm long, 1.5–3 cm wide, the upper ones somewhat shortened, the terminal 1½–2 × the length of the basal pinnae, only in plurijugate leaves of comparable size. Lamina of simply pinnate leaves similar to the primary pinnae of bipinnate ones. Secondary rachises (and primary of once-pinnate laminae) brown or reddish, adaxially flattened, with sharp borders, abaxially with a short terete basal portion, from the level of the first to third pinnule with sharp, paler at the base almost always irregularly interrupted angles which above are mostly somewhat wing-like. Pinnae slightly narrowed at the base, gradually narrowed from somewhat above the base to the apex. *Pinnules* up to ca. 80 to a side, mostly less, subopposite to alternate, subsessile, spreading or the basal ones usually somewhat falcately deflexed, remote, the upper ones gradually closer, contiguous or slightly imbricate, 5–14 mm long, 3–7 mm wide, mostly hardly narrowed to the broadly rounded apex. Inner margin straight, parallel or slightly divergent from the sec. rachis, upper base shortly rounded to almost rectangular, lower base shortly cuneate, hardly stalk-like, lower margin concave in the inner, faintly concave or straight in the outer part, upper margin approximately straight in the inner, convex in the outer part, sometimes almost angularly passing into the outer margin, minutely crenate or subentire in fertile pinnules, shallowly crenate or sinuate, less often dentate or denticulate, in sterile ones, sometimes crispate, occasionally revolute around the sorus. Marginal thickening stramineous, rather conspicuous throughout, sometimes remaining in withered leaves where the leaf-tissue has decayed. Veins elevated and stramineous at their bases on both sides, otherwise immersed but visible as wrinkles in the leaf-tissue in dried specimens, mostly two or three times forked, rather close, their ends ½–¾ mm apart; main vein only shortly continuous with the marginal strand but close to it, ca. ¼ mm above it near the apex. Upper pinnules gradually reduced, 2–4 mm long, one or two connected by a wing with the terminal segment which is lanceolate, subacute, ½–1½ cm long, crenate or lobed at the often soriferous base. *Sori* along the upper and outer margin; indusium thin, pale, ca. 0.3 mm wide, not reaching the margin by a distance of 0.3–0.5 mm, strongly reflexed and ± conceiled at full maturity. Simply pinnate leaves are often sterile in the lower half or third. Sporangia ca. 175–190 × 140 μ; annulus with 8–10 indurated cells; spores medium brown, ca. 27–36 μ.

Distribution: Almost throughout the range of the genus in the New World, but so far not collected in the Lesser Antilles and most of Central America; commonest in the Greater Antilles and the Guianas, including Trinidad (map 25). One of the very few euryoeceous species; in moist forests, in thickets, swamps, among rocks, on banks of roads, on exposed sandy soil, sometimes on laterite, etc., from sea-level to about 1200 m.

Representative specimens:

CUBA: Pinar del Rio, Wright 3948 (B, GH, K, NY, S–PA, US).

HISPANIOLA. SAN DOMINGO: Samaná Penins., Jato Viejo, Abbott 1334 (GH, US); Liali, Abbott 2589 (C, GH, US); Cordillera Septentrional, Matanzas, Sabana de los Gengibres, Ekman H 15869 (C, G, K, S).

JAMAICA: Pedro Morass, near Clarendon, Harris 11165 (BM, C, F, GH, K, MO, NY, US); Tea Gully, near New Market, Harris 9911 (BM, C, F, K, NY, US);

Bluefield Mts., Purdie s.n. (BM, K); Bull Head, Clarendon, Sherring 393 (BM, K). Puerto Rico: Near Dorado, Britton, Britton & Brown 6647 (F, G, NY, PH, US); Utuado, Sintenis 6382 (B, BM, MO, US); Aguada, Piedra Blanca, Sintenis 5709 (B, BM, BR, C, F, G, GH, K, L, LE, M, MO, NY, PH, S-PA, US, W); Vega Baja, Heller & Heller 1312 (F, K, NY, US).
Mexico. Vera Cruz: Minatitlan, J. G. Smith 57 (MO, US).
Oaxaca: Talea, Galeotti 6470 in part (B, BR, W); without loc., Galeotti 6495 in part (FI, W).
British Honduras: Boomtown, O'Neill 8411 (F, GH, NY, S–PA, UC); Cow-Pen near Monkey River, Gentle 4128 (GH, MO, NY, US).
Guatemala: Zacapa, Palmilla, Walker s.n. (Donnell Smith 1203) (US).
Colombia. El Valle: Buenaventura, Killip 11739 (US).
Meta: Villavicencio, Hacienda San Carlos, Hermann 11139 (US).
Chocó: La Equis, Molina & Barkley 19 Ch 069 (K); Lloró, south of Quibdó, Archer 2063 (US).
Venezuela. D.F.: Caracas, Karsten s.n. (W).
Amazonas: La Esmeralda, Croizat * 164 (U).
Trinidad: Valencia, Britton, Britton & Hazen 1016 (GH, NY, US); Sangre Grande, Broadway 5381 (F, MO, U, UC, US); Aripo Road, Broadway 8025 (BM, G, MO, S); Long Stretch, Hombersley 73 (K).
British Guiana: Kaieteur Savanna, Jenman 1386 (K); Rockstone, Gleason 603 (GH, K, NY, US); Kamakusa, Leng & Persaud 368 (F, NY, US); Parabaru Savanna, A. C. Smith 3056 (F, G, GH, K, NY, U, US); Forest Station, Mazaruni R., Forest Dept. 6896 (K, U); ibid., Fanshawe M 334 (K, U); without loc., Schomburgk 274 in part (B, Holotype of *L. crenata*); Schomburgk 346 in part (B, Holotype of *L. rufescens*; Isotypes in BM, FI, G, L).
Suriname: Near plant. Onoribo, Para R., Focke 913 (K, U); Para Distr., Hostmann & Kappler 1738 (B, G, FI, LE); Paramaribo, plant. Jagtlust, Suringar 6092 (L); Upper Sipaliwini R., Tumuc Humac Range, Rombouts 403 (U).
French Guiana: Oyor, Leprieur 18 (B, GH, LE, NY, US); Montsinéry, near Cayenne, Leprieur 67 (G); Cayenne, Sagot 1363 (B, BM, K, S–PA); ibid., Leprieur 168 (FI, NY, P, U), Baduel, near Cayenne, Broadway 909 (GH, K, NY, US).
Brazil. Amazonas: Near Panuré, Rio Uaupés, Spruce 2325 (BM, G).
Bahia: Ilheos, Riedel s.n. (L); ibid., Blanchet 2 (G).
Minas Gerais: Corrego Fundo, C. Verde, Macedo 3378 (MO, US).
Rio de Janeiro: Serra dos Orgãos, Burchell 2663 (B, K, US); Rio Maná, Spannagel 534 (UC); Tijuca, Miers 136 (BM); ibid., L. B. Smith & Brade 2202 (GH, US); Jacú, Glaziou 2805 (B, BR, C, K, S, Isotypes of *L. consanguinea* var. *rigida*).
São Paulo: Serra São João, near Santos, Wettstein & Schiffner s.n. (W).
Bolivia. Santa Cruz: Buena Vista, prov. del Sara, Steinbach 2200 (B, GH, S–PA, U).

The simply pinnate forms of this species are sometimes difficult to separate from *L. stricta*, probably its closest relative. *L. stricta* has smaller, thicker pinnules with obscure veins and the rachis is abaxially at least for a considerable basal part terete, but there are a few intermediates, e.g. Ekman H 9021 (C. Chr. in BM, K, NY, S, US) from Massif de la Hotte, Haïti, Hispaniola, which are difficult to assign to either of the two species. There is probably some hybridization; they often occur in the same sort of habitat and are frequently collected together.

27. **Lindsaea stricta** (Swartz) Dryander, Trans. Linn. Soc. 3:42 (1797); Roem. Arch. 2 (II): 237 (1801); Swartz, Syn. Fil. 119 (1806); Schkuhr, Krypt. Gew. I:105 (1809), t. 114; Willdenow, Spec. Pl. V:425 (1810); Presl, Rel. Haenk. I:59 (1825); Sprengel,

Syst. Veg. IV: 80 (1827); Desvaux, Prod. 313 (1827); Presl, Tent. Pterid. 131 (1836); Gardner, Lond. Jo. Bot. 1:200 (1842); J. Smith, ibid.: 200 (1842); Hooker, Spec. Fil. I:216 (1844), p.p. mai.; Liebmann, Vid. Selsk. Skr. 5 (1):269 (1849); Kunze, Bot. Zeit. 8:371 (1850); Mettenius, Ann. Sci. Nat. 5e sér. 2:216 (1864); Ettingshausen, Farnkr. t. 142 fig. 4, 145 fig. 5–8, 14 (as *guianensis*), 146, fig. 8, 19, 20 (1865); Wawra, Bot. Ergebn. Max. Reise Südbras. 192 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 108; Fée, Crypt. vasc. Brés. I:30 (1869); Baker, Fl. Bras. I^2:353 (1870), t. 21 fig. 22–25; J. Smith, Hist. Fil. 268 (1875); Eaton, Bot. Gaz. 3:91 (1878); Kuhn, Chaetopt. 26 (1882); Jenman, Jo. Bot. 25:98 (1887); O. Kuntze, Rev. Gen. Pl. 815 (1891); Eaton, Mem. Torr. Bot. Cl. 4 (3):272 (1895); Schenck, Hedwigia 35:158 (1896); Christ, Farnkr. d. E. 293 (1897); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p. p. mai.; Wright, Trans. Linn. Soc. II, 6:80 (1901); Diels, N. Pfl. I^4:221 (1902); Rosenstock, Hedwigia 46:80 (1906); Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. VII:343 (1918); Urban, Symb. Ant. 9:322 (1925); Knuth, Fedde Rep. Beih. 43 (1):32 (1926), p. p. mai.; Posthumus, Fl. Surin. Suppl. 74 (1928); Domin, Pterid. Domin. 242 (1929); Standley & Record, Field Mus. Publ. 350:64 (1936); Weatherby, Contr. Gray Herb. 114:26 (1936).

Basionym: *Adiantum strictum* Swartz, Prodr. 135 (1788); J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:413 (1793); Poiret in Lamarck, Encycl. Suppl. I:140 (1810).

Type: Swartz s.n. from Jamaica (S-PA!).

Homotypic synonym: *L. guianensis* (Aubl.) Dryand. f. *stricta* (Sw.) Lindman, Ark. f. Bot. I:201 (1903), pl. 8 fig. 4 a, b.

Heterotypic synonyms: *L. elongata* Cavanilles, Descr. 265 (1802). Type: "Don Luis Née, Panamá; tambien se cria en Puerto-Rico" (MA? not seen).

L. rigescens Willdenow, Spec. Pl. V:421 (1810); Desvaux, Prod. 313 (1827); Presl, Tent. Pterid. 131 (1836); Klotzsch, Linnaea 48:546 (1844); Fée, Crypt. vasc. Brés. I:29 (1869), in part. Type: Bredemeyer s.n. from Caracas, Venezuela (W!).

L. brasiliensis Desvaux, Berl. Mag. 5:330 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936). Type: Unknown coll., "habitat in Brasilia" (P!).

L. elata Desvaux, Berl. Mag. 5:326 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936). Type: Unknown coll., "habitat in Caribaeis" (P!).

L. imbricata Desvaux, Berl. Mag. 5:326 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936); non Liebmann, 1849. Type: Unknown coll., "habitat in America?" (P!).

L. microphylla Presl, Rel. Haenk. I:59 (1825), non Swartz 1800. Type: Haenke s.n. from Mexico (prob. PR; not seen).

Homotypic synonyms: *L. stricta* (Sw.) Dryand. var. *microphylla* (Pr.) Hassler, Trab. Inst. Farm. Buenos Aires 25:36 (1928).

L. parvifolia Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:207 (1844).

L. elegans Hooker, Icon. Plant. t. 98 (1837); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930), pl. 12, fig. 3; non Fée, 1852. Type: Cuming 1101 from Colombia (K!).
Homotypic synonyms: *L. guianensis* (Aubl.) Dryand. var. *elegans* (Hook.) von Luetzelburg, Est. Bot. Nordéste Bras. 3:245 (1923).
L. stricta (Sw.) Dryand. var. *elegans* (Hooker) [incorr. attributed to C. Christensen by] Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930).

L. Raddiana Klotzsch, Linnaea 18:549 (1844); Fée, Crypt. vasc. Brés. I:30 (1869). Type: Schomburgk 253 in part, from British Guiana (B!).

L. stricta (Sw.) Dryand. var. *β tripinnata* Hooker, Spec. Fil. I:216 (1844). Type: Gardner 5323 from Cocaes, Minas Gerais, Brazil (K!).

L. multifrondulosa Fée, Gen. Fil. 105 (1852), t. 28. fig. 1; 11^{e} mém. 17 (1866). Type: Galeotti 6470 in part, from Oaxaca, Mexico (P!).

L. dentata Fée, Crypt. vasc. Brés. II:20 (1872/73). Type: Glaziou 5357, from Corcovado, Rio de Janeiro, Brazil (P!).

L. portoricensis Desv. var. *brachypoda* Domin, Pterid. Domin. 243 (1929). Type: not indicated; three coll. cited: Sherring s.n. from Bull Head, Jamaica, Fendler 89 from Trinidad, and Kalbreyer 1423 from Antioquia, Colombia. The second coll. is most eligible as type; if there is a specimen in PR, that should be the lectotype; otherwise the specimen in K.

Misapplied names: *L. javitensis* auct. non H. & B. in Willd.; Raddi, Opusc. Sci. Bol. 3:294 (1819); Plant. Bras, nov. gen. spec. 56 (1825).

L. guianensis auct. non Dryand.; Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.; Christ in Pittier, Prim. Fl. Costar. 3:37 (1901); Rosenstock, Hedwigia 46:80 (1906); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930.

Petioles pale or dark, abaxially terete; lamina simply pinnate, bipinnate with conform terminal pinna, or occasionally tripinnate, herbaceous to coriaceous; pinnules close, roundish or oval to rounded-subtrapeziform, as long as to 1½ × as long as wide; veins immersed, mostly obscure; upper pinnules gradually and strongly reduced; sori continuous, often absent from the lower part of the lamina, especially in simply pinnate leaves; indusium mostly strongly erose to lacerate; spores trilete.

Rhizome creeping (often widely), 1–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2 mm long, 0.3 mm wide, with up to 8 rows of cells at the base (relatively narrowest in specimens from exposed habitats) (fig. 2). *Petioles* mostly rather close or close, adaxially flattened or broadly and shallowly sulcate towards the apex. *Primary rachis* of more than once pinnate leaves abaxially terete or slightly flattened. Axillary cushions visible as slightly discoloured spots or obsolete. *Pinnules* rather close to contiguous or slightly overlapping. Veins immersed except at their extreme bases, once or twice forked, their ends ca. ½ mm apart. Upper pinnules gradually reduced, 1–3 mm long, one or a few connected with the small elliptic-lanceolate or roundish terminal segment. *Sori* around the upper/outer margin; indusium stiff, 0.3–0.5 mm wide, not reaching the margin by 0.2–0.4 mm. Spores medium brown, ca. 35 μ.

This very widespread species consists of three rather clear-cut varieties which can be distinguished as follows:

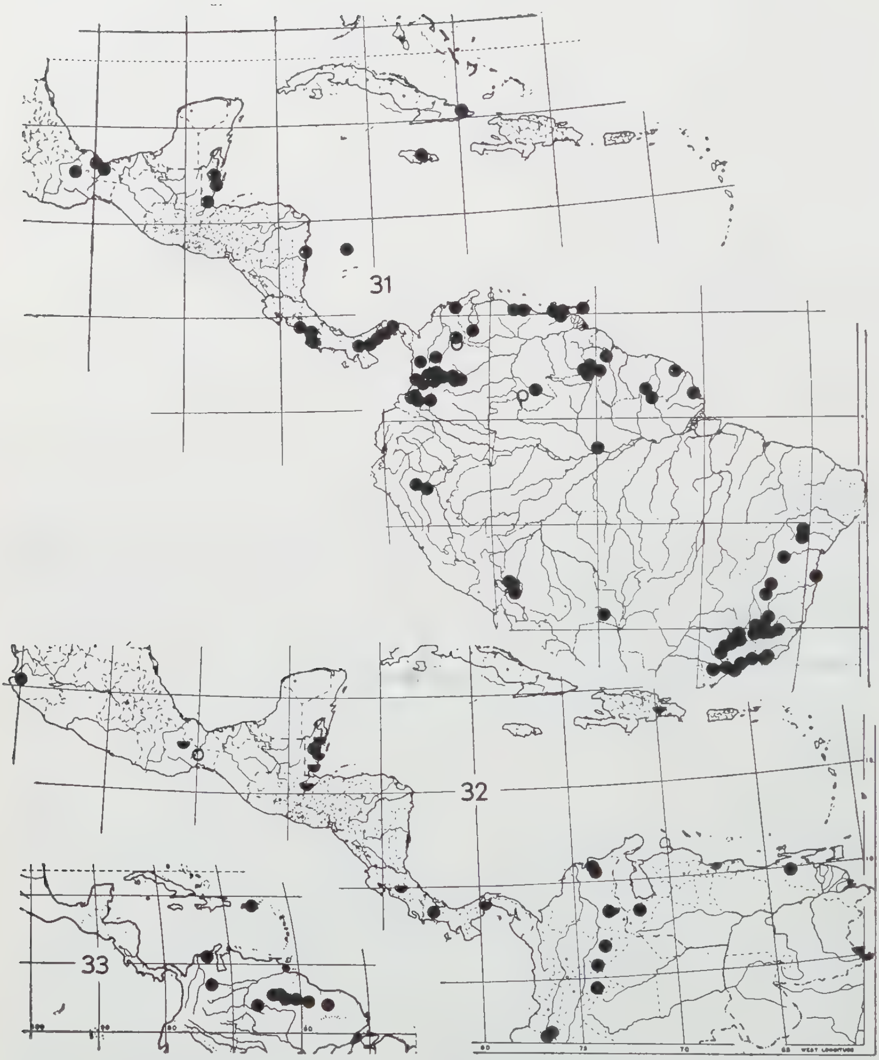
1. a. Upper part of the petiole, primary rachis at least near the nodes and secondary rachises at least at the base with thick laterally projecting ridges on the adaxial side, visible from the abaxial side; mostly bipinnate . . . . . b. var. *parvula*
   b. Axes without these ridges 2

2. a. Primary rachis of simply pinnate leaves and secondary rachises of bipinnate leaves abaxially angular to the base or almost to the base, flattened or convex between the angles, red to blackish; leaves very coriaceous, pinnate, or bipinnate with ascending pinnae . . c. var. *jamesoniiformis*
   b. Primary and secondary rachises abaxially at least in a considerable basal portion terete, rarely the greater part angular or sulcate, stramineous or pale brown; leaves herbaceous to coriaceous, once or twice, rarely three times pinnate a. var. *stricta*

a. var. **stricta f. stricta.** **Fig. 26, 73**

Petioles ca. 2–30 cm long, ¾–1.5, mostly 1 mm in diam. near the apex, stramineous to pale brown, or, especially in simply pinnate leaves, tinged with red (mostly less than in *L. portoricensis*), rarely castaneous to blackish, dull or ± shining, abaxially almost always quite terete. Length-ratio petiole : lamina very variable, the petiole from as long as to more than 10 × as long as the lamina. *Lamina* pinnate or bipinnate (very often on the same rhizome), rarely subtripinnate or fully tripinnate, chartaceous to coriaceous (herbaceous in the form discussed below), mostly yellowish green, up to ca. 70 cm long, with one odd up to 6 pinnae to a side when more than once pinnate. *Primary rachis* of more than once pinnate leaves similar to the petiole. *Pinnae* (if any) subopposite or alternate, mostly strongly ascending, parallel to each other or ± contiguous, sometimes spreading in amply bipinnate leaves, the largest ca. 1.5–4 cm apart, the upper ones gradually closer, subsessile or the terminal stalked (up to 2 cm), the lower ones ca. 10–25 cm long, (¾–)1–1.5(–2) cm wide, the upper ones somewhat shorter, the terminal longest in paucijugate leaves. Secondary rachises and rachis of simply pinnate leaves adaxially very shallowly sulcate, the groove hardly concave, abaxially terete in the lower third or often considerably more (rarely less), in the upper part gradually obtusely, then sharply angular, sulcate only near the apex. *Pinnules* ca. 25–70 to a side, the basal ones of simply pinnate laminae and of terminal pinnae, rarely also of lateral pinnae, more remote and/or strongly deflexed, otherwise spreading or slightly deflexed, subsessile, glossy when thick in texture, 4–8 mm long, 3–5½ mm wide; a strongly reduced axillary pinnule present, one or two adjacent pinnules sometimes ± reduced, those in the upper half or one-third of the lamina gradually reduced. Inner margin faintly convex, mostly somewhat divergent from the rachis, lower base hardly cuneate, not stalk-like, upper base shortly rounded or almost rectangular, upper margin convex, more strongly so towards the apex, lower margin straight or, at least in the basal part, concave, apex broadly or shortly rounded, a separate outer margin hardly ever developed. Marginal thickening visible throughout, conspicuous especially along the lower margin, stramineous or pale brown, entire or minutely repand-erose along the soriferous margins, in withering leaves sometimes remaining when the leaf-tissue has dropped out. Sterile pinnules entire or shallowly sinuate or subdentate with small obtuse teeth along the upper/outer margin; fertile pinnules quite entire, apart from the erose marginal strand. Terminal segment 0.4–1 cm long, triangular-lanceolate, obtuse or subacute, soriferous at the base, sometimes also around the apex. Leaf- and pinna-apices often absent in dried specimens, probably remaining immature for a long time and lost in pressing or mounting. Sporangia ca. 195 × 158 μ; annulus with 13–15 indurated cells.

This description applies to the commonest form. In South America,



Maps 31–33: *L. stricta;* map 31: var. *stricta* f. *stricta;* map 32: complete dots: f. *moritziana;* half dots: intermediates between f. *stricta* and f. *moritziana;* map 33: var. *jamesoniiformis.*

particularly in south-eastern Brazil, a large, mostly bipinnate or subtripinnate form occurs with chartaceous or quite herbaceous pinnules which are distinctly crenate or sharply dentate when sterile, often sharply erose-denticulate when fertile; the pinnae are more spreading than mostly in the other form (fig. 73). These specimens have been described as *L. brasiliensis* Desv. and *L. dentata* Fée, and have often been misidentified as *L. guianensis;* because of this, Lindman considered

L. stricta to be only a form of *L. guianensis*. The latter species has, however, narrower, entire or minutely erose indusia, and ssp. *guianensis*, which may be more or less like *L. stricta*, has long-caudate or acuminate pinna-apices. Extreme specimens of the lax form of *L. stricta* look rather different, but there is a large series of intermediates with the typical form, and both are united here under var. *stricta*. Typical specimens of the lax form are marked with an * in the enumeration of specimens.

Distribution: Widespread and common almost throughout tropical America, but rare in most regions where the following variety occurs (map 31). On campos and savannas, on rocky slopes, in scrub, in forest-clearings, in crevices of rocks (sandstone, granite, rarely limestone); the lax form in more shaded situations, in light forests; from sea-level to almost 2000 m.

Vern. name: cumyaic (Boz, Brit. Guiana).

Representative or widely distributed specimens:

MEXICO. OAXACA: Between Comaltepec and Trapiche de la Concepcion, Liebmann 2448 (C); without loc., Galeotti 6470 in part (P, HOLOTYPE of *L. multifrondulosa*; Isotypes in B, G, LE).

VERA CRUZ: Chinameca, Orcutt 3197 (BM, GH, K, MO, US).

BRITISH HONDURAS: Stann Creek Railway, Schipp S 28 (B, F, US); Pine Ridge, Yaccos Lagoon, Peck 677 (F, GH, K, US).

NICARAGUA: Wuonta-Haulover, Schramm 27 (S–PA).

COSTA RICA: Los Palmares, Pittier s.n. (BR, US); Buenos Aires-Osa, Valerio 1822 (US).

PANAMÁ: Las Margeritas-El Valle, Woodson, Allen & Seibert 1278 (MO, NY, US); below Bismark, R. S. Williams 505 (NY, US); Hacienda de la Joya, Panamá prov., Dodge, Hunter, Steyermark & Allen 16883 (G, MO, US).

CUBA. ORIENTE: Airport, vic. of Moa, Acuña 12352 (US).

JAMAICA: Frankfield to Cave Valley, Orcutt 7833 (G, K, MO, UC, US); Bunker's Hill Savanna, Harris 11171 (BM, F, K, MO, NY, US); Bull Head Mountain, Sherring s.n. (K, Paratype of *L. portoricensis* var. *brachypoda*); without loc., Swartz s.n. (S–PA, HOLOTYPE; Isotype in M; fragment and photogr. in US).

ISLA DE PROVIDENCIA (to Colombia, 13°21′ N, 81°23′ W): Summit of highest peak, Proctor 3392 (PH, US).

COLOMBIA. MAGDALENA: Sierra Nevada, Bolinder s.n. (C, S–PA).

CHOCÓ: La Oveja–Quibdó, Archer 1761 (GH, US).

EL VALLE: Buenaventura, Killip 5320 (GH, K, NY, PH, US); Pavas, Pennell 5498 (GH, NY, PH, US); Cali, André 448 (F, K, NY).

CAUCA: Aganche, Pennell & Killip 6283 (US); El Ramal–Río Sucio, w. of Popayan, Pennell & Killip 8134 (GH, NY, PH, US); El Hatico, Lehmann 6076 (B, K, LE, US); Río Piendamo, André 2743 (F, GH, K, NY, US).

NORTE DE SANTANDER: Ocaña, Karsten s.n. (W).

SANTANDER: Mesa de los Santos, Killip & A. C. Smith 15337 (GH, NY, US); Socorro, Lindig 47 (K).

META: Llanos de San Martín, Stübel 710 (B).

CUNDINAMARCA: Cerinza, e. of Gutiérrez, Grant 9762 (US); Bogotá, Karsten 47, 62 (B).

TOLIMA: El Convenio, w. of San Lorenzo, Pennell 3485 (F, GH, K, MO, NY, US).

CAQUETÁ: Florencia–Cordoba, Juzepczuk 6486 (US).

ANTIOQUIA: Canoas, Kalbreyer 1423 (B, K).

Without loc., Cuming 1101 (K, HOLOTYPE of *L. elegans* Hook.).

VENEZUELA. SUCRE: Valley of Cocollar, Steyermark 62382 (F, US).

D.F.: Caracas, Aldridge s.n. (NY); ibid., Bredemeyer s.n. (W, very probably type-material of *L. rigescens*); Cerro de Macarao, Tamayo 4174 (U, US).

MÉRIDA: Near Tovar, Fendler 377 (B, BR, C, F, G, GH, GOET, K, MO, PH, US); ibid., id. 479 (G, GH, GOET, K, MO, PH).

Monagas: La Sabana de las Piedras–Cerro Negro, n.w. of Caripe, Steyermark 61806 (F, US).

Bolívar: La Gran Sabana, R. Uairén, Sta. Elena, Tamayo 2836 (US).

Amazonas La Esmeralda, Upper Orinoco, Ll. Williams 15390, 15432 (US); Esmeralda Ridge, Tate 232 (NY).

State?: Near San Antonio, Otto 695 (B, BM, G, K, L, LE, S–PA, W).

Trinidad: Without loc., Fendler 89 (B, BM, F, G, GH, IA, K, LE, M, NY, PH, UC, US); Lockhart s.n. (GH, K).

British Guiana: Paramacutoi Savanna, Ireng Distr., Boz 523 (C, K); Mazaruni Station, Fanshawe M 240 (BM, K, U); Mt. Roraime, Tate 310 (NY, US).

Suriname: Palaime Savanna, Paloemeu R., Geyskes s.n. (U).

French Guiana: Montsinéri near Cayenne, Leprieur 50 (B, LE, US), 161 (FI, G).

Brazil. Bahia: São Bento, von Lützelburg 113 * (M, NY); Ilheos, Riedel s.n. * (B, GH, S–PA); ibid., Blanchet 3471 (K, MO); ibid., Riedel s.n. (B, FI, G, LE, S–PA, UPS, W).

Rio Branco: Igarapé, Rio Quinô, von Lützelburg 21356, 21536 (M).

Amazonas: Manáos, Cachoeira Grande, Schwacke III 189 (GOET).

Pará: Upper Parú, Sampaio 5578 (B).

Amapá: Cunani, Huber 1113 (G).

Goias: Without loc.; Glaziou 22640 (B, G, NY).

Minas Gerais: Viçosa, Mexía 5486 * (B, BM, C, F, G, GH, K, MO, NY, PH, S, U, UC, US); São João del Rei, Lindman A 141 * (K, S, S–PA, UPS); near Cocaes, Gardner 5323 * (K, Holoytpe of var. *tripinnata*; Isotypes in B, BM, FI, G, W); Ouro Preto, Itacolomi, Macedo 2765 * (MO, US); Caraça, Mendonça 420 (B); Serra do Ouro Branco, Schenck 3538 (B).

Rio de Janeiro: Near Rio, Mosén 74 * (B, BR, FI, K, LE, M, S, U); Serra de Estrella, Brade s.n. (NY, UC); Serra dos Orgãos, von Lützelburg 487 (M, S–PA); Corcovado, Mosén 2640 * (C, S, S–PA, UPS); ibid., Pohl sn. * (W).

São Paulo: Rio Grande, Wacket s.n. (Rosenstock-exs. 67) (B, F, M, S, S–PA, US, W); Retiro da Lagem near Cajurú, Regnell III 1474 (B, BR, C, LE, S, S–PA, UPS, US); Ilha de São Amaro near Santos, Wettstein & Schiffner s.n. (W); Santa Anna, Brade 5176 * (NY, UC); Campinas, Heiner s.n. * (S, S–PA); São José do Barreiro, Hoehne & Gehrt 17697 * (BM, GH), near Santos, Burchell 3240 (B, FI, GH, K, L, LE, US, W).

Matto Grosso: Without loc., H. Smith Jr. s.n. * (UC).

Santa Catarina: Without loc., Macrae s.n. (B).

Perú. San Martín: San Roque, Ll. Williams 7760 (F, GH); Lamas, Ll. Williams 6382 (F, US); Zepelacio near Moyobamba, Klug 3418 (B, F, G, GH, K, MO, NY, S, US).

Bolivia: Songo, Bang 905 (B, BM, G, GH, K, LE, M, MO, NY, PH, US, W); near Atan, R. S. Williams 1332 (GH, NY, UC, US); n. of Santiago de Chiquitos, Cutler 7029 (US); San Antonio near Mapiri, Buchtien 1106 * (NY, S–PA, US); Tipuani Valley, Hacienda Casana, Buchtien 7068 * (G, MO, NY, S–PA, UC); Apolo, R. S. Williams 1330 * (GH, NY, UC, US); Cerro Amboró, Herzog 576 * (B).

A specimen collected by Tweedie labelled "Tucumán" in LE; this locality is probably incorrect, as the species has never again been found in this rather well-collected part of Argentina.

Another aberrant form is found in Central and north-western South America (map 32). It differs from the typical form in several characters considered characteristic of *L. stricta* and would be excluded from that species if it were not for a number of intermediates in the same area which link it with typical *stricta*. It may be distinguished as forma **moritziana** (Klotzsch) Kramer, comb. nov.

Basionym: *L. Moritziana* Klotzsch, Linnaea 18:548 (1844), in part.

Lectotype: Moritz 164 in part from Caripe, Venezuela (B!); of the other specimens cited, the second, Schomburgk 272 from British

Guiana was not seen by the present author; the third, Schomburgk 273 in part, also from British Guiana, belongs to *L. guianensis*.
Homotypic synonym: *L. guianensis* (Aubl.) Dryand. var. *β major* Hooker, Spec. Fil. I:217 (1844).

Petiole stramineous or pale brown, abaxially often obtusely or even sharply angular or sulcate above, rarely close to the base, then castaneous; *primary rachis* abaxially at least obtusely, often sharply angular, or sulcate; *lamina* bipinnate or subtripinnate, with mostly patent, often decurved pinnae; secondary rachises abaxially terete at the extreme base only, otherwise flattened, angular or sulcate, often more slender than in the typical form; *pinnules* herbaceous or chartaceous, never coriaceous, not rarely more elongate than in the typical form; indusium often less erose, often subentire.

Typical specimens are:

Mexico. Oaxaca: Without loc., Galeotti s.n. (FI).
Jalisco: Sierra Madre Occidental, Hacienda del Ototal w. of San Sebastian, Mexía 1837 (F, G, GH, MO, NY, UC, US).
British Honduras: Gracie Rock Pine Ridge, Sibun R., Gentle 1536 (GH, K, MO, NY, UC, US).
Costa Rica: Without loc., Endres 16 (BM, W).
Panamá: Cerra Vaca, Chiriquí prov., Pittier 5368 (US); Boquete, ibid., Davidson 837 (F, GH, MO, US).
Colombia. Magdalena: Santa Marta, Mt. Cuaco, H. H. Smith 938 (BM, F, GH, K, MO, NY, PH, S–PA, US); ibid., Las Partidas, H. H. Smith 1089 (NY); ibid., Dos Aguas, Carriker 27 (US); Santa Marta, Purdie s.n. (BM).
Cauca: Tetilla near Popayan, Stübel 88 (B); El Tambo, Kj. von Sneidern 2181 (G, S).
Norte de Santander: Ocaña, Kalbreyer 399 (B, K).
Santander: Socorro, Karsten s.n. (W); ibid., Lindig 62 (B, BM, K).
Cundinamarca: Bogotá, Karsten 63 (B).
Boyaca: Puente Nacional, Karsten s.n. in part (LE); Cune, Lindig 63 (B, BM).
Without loc., Lehmann 5030 (F, K, US).
Venezuela. Mérida: Between Maracas and Chorona, near Tovar, Fendler 378 in part (BR, G, K); ibid., id. 380 (B, GOET, K).
Monagas: Caripe, Moritz 164 in part (B, Holotype; Isotype in BM).

As intermediates between f. *moritziana* and f. *stricta* may be cited (map 32):

Mexico. Oaxaca: Choapam, Yaveo, Mexía 9138 (B, F, G, GH, K, MO, NY, Pic.-Ser., S–PA, U, UC, US).
British Honduras: Manatee Pine Ridge, Belize distr., Gentle 89 (US); Sarawee Pine Ridge, Stann Creek distr., Gentle 2698 (NY, US); Monkey River, Toledo distr., Gentle 3687 (GH, K, MO, NY).
Guatemala: N. of Quiriguá, Weatherwax 225 (MO).
Honduras: Without loc., Berry s.n. (IA).
Costa Rica: Near El General, San José prov., Skutch 4105 (BM, K, MO, NY, S–PA, US).
Colombia. Norte de Santander: Ocaña, Schlim 53 p.p. mai (BR, FI, G, GH, L, W).
Venezuela. Aragua: Near Choroni, Vogl s.n. (M).
Brazil. Rio Branco: Igarapé of Rio Quinô, von Lützelburg 21364 in part (M); summit of Mt. Roraima, von Lützelburg 21609 (M).
Hispaniola. San Domingo: Bayaguana, slope of Loma Managuá, prov. San Domingo, Ekman H 11100 (B, F, GH, K, NY, S, UC, US).

b. var. **parvula** (Fée) Kramer, comb. nov. **Fig. 74**

Basionym: *L. parvula* Fée, 11e mém. 17 (1866), Hooker & Baker, Syn. Fil. 1st ed. 452 (1868), 2dn ed. app. 471 (1874); Jenman, Jo. Bot. 25:98 (1887); W. Ind. Gui. F. 78 (1899); Diels, N. Pfl. I^4:221 (1902); Knuth, Fedde Rep. Beih. 43 (1):32 (1926).
Type: Germain s.n. from Trinidad (P!).

Heterotypic synonyms: *L. gracilis* Klotzsch, Linnaea 18:549 (1844), non Blume 1828. Type: Schomburgk 273 from British Guiana (B!).

L. aquatica Jenman, W. Ind. Gui. F. 78 (1899). Type: Jenman s.n. from Macouria Creek, Essequibo R., British Guiana (NY!, 2 sheets).

Petioles ca. 10–60(–80) cm long, slightly shorter than to almost 3 × as long as the lamina, ⅔–1¾, mostly 1–1½ mm in diam. near the apex, stramineous or less often reddish-brown, dull or somewhat shining, adaxially flattened almost to the base, broadly and shallowly sulcate above, with obtuse angles, abaxially terete but often flattened above, near the apex with lateral ridges as described for the rachises. *Lamina* bipinnate, rarely simply pinnate on mature rhizomes, ca. 10–35(–60) cm long, firmly herbaceous to chartaceous or mostly coriaceous, dark brownish to dark yellowish-green, paler on the dorsal side, with from one odd to 9 primary pinnae to a side and a conform terminal one. *Primary rachis* adaxially mostly with a deeper groove than the petiole, abaxially terete or slightly flattened with rounded angles, laterally near the adaxial surface with a groove which runs below the edges of the adaxial groove which are visible as ledges from the abaxial side (Fig. 7); these may be evident at the nodes only, sometimes only in the lower part of the primary rachis, and are occasionally conceiled by the bulging lateral surfaces (see also p. 114 and fig. 74). Axillary cushions hardly or not swollen but usually visible as small dark dots. *Pinnae* mostly subopposite, mostly strongly ascending, often contiguous, 2–7(–9) cm apart, the upper ones sometimes closer, mostly about 7–12(–30) cm long, 0.5–1(–1.5) cm wide, the upper ones shorter in plurijugate leaves, the terminal longest in paucijugate ones, practically sessile or the terminal one with a stalk of 0.5–2 cm, linear, gradually narrowed from just above the base to the long-acuminate apex. Secondary rachises (and rachis of simply pinnate leaves) adaxially with a rather wide and deep channel, abaxially round at the base, then angular, finally narrowed and sulcate, the relative length of these portions quite variable; lateral surfaces channelled in the same way as described in the primary rachis at least at the base. *Pinnules* ca. 25–60 (rarely up to ca. 100) to a side, alternate or the lower ones subopposite, mostly not contiguous, roughly oval, 3–6 mm long, 2–4.5 mm wide, spreading, often laxly ascending or the lower ones slightly deflexed; a strongly reduced axillary pinnule present, one or two additional pinnules on the acroscopic side may be slightly reduced. Basal pinnules of simply pinnate blades not reduced. Inner margin straight or somewhat convex, often touching or overlapping the rachis, lower base very shortly cuneate, hardly stalk-like, upper base of pinnules shortly rounded, lower margin mostly shallowly S-shaped, rarely more strongly concave, upper margin evenly rounded or more convex towards the apex; apex of pinnules rounded. Marginal thickening stramineous, conspicuous, especially on the abaxial side, erose in fertile pinnules, subentire to faintly sinuate or repand along the upper/outer margin in sterile ones. Veins sometimes slightly elevated. Terminal segment up to 7 mm long, 3 mm wide. Sori not rarely conceiled by the incurved margin; indusium strongly reflexed and conceiled at full maturity. Sporangia ca. 185 × 160 μ; annulus with 11–13 indurated cells; spores 32?

Distribution: Mostly confined to northern South America; most common in Trinidad and the Guianas (map 34). Almost always in moist places in savannas, in bogs, and along watercourses; rarely in forests or among rocks. Elevations not indicated, but probably restricted to lower altitudes (below 1000 m).

Vern. name: Koeliki kaloeabandikoro (Arowakkan, Suriname).

Representative specimens:

Cuba. Oriente: S. side of Bahia de Moa, Howard 5897 (GH, MO, NY, U).
British Honduras: All Pines, Schipp S 197 (B).
Nicaragua: Wuonta–Haulover, Schramm 34 (S–PA); Mosquito-coast, Wullschlaegel s.n. (B).
Colombia. Chocó: Quibdó, Río Atrato, Archer 1770 (NY, US).
Meta: R. Zanza–R. Güejar, n. end of Cordillera Macarena, S. G. Smith & Idrobo 1547 (UC, US).
Trinidad: Aripo Savanna, Britton & Britton 2927 (GH, K, NY, US); ibid., Broadway 2406 (BR, G, MO, S–PA, US), 5283 (F, MO, U, UC); ibid., Fendler 89β (B, GH, LE, MO, NY, US), and several other collections; Arima, Woodford 58 (K); without loc., Germain s.n. (P, Holotype).
British Guiana: Kamakusa, Upper Mazaruni R., de la Cruz 4066 (F, GH, MO, NY, PH, UC, US); Mazaruni Station, Sandwith 1014 (BM, K); ibid., Fanshawe M 332 (K); Macouria Creek, Essequibo R., Jenman s.n. (NY, 2 sh., Holotype of *L. aquatica*); without loc., Schomburgk 273 (B, 3 sh., Holotype of *L. gracilis* Kl.; Isotype in BM).
Suriname: Line Moengo tapoe–Grote Zwiebelzwamp, Lanjouw & Lindeman 568, 726, 767, 795, 1012 (U); Couroupina Creek, Kappler 1737 (B, C, FI, G, MO); Cordonpad near Joden-Savanna, Kegel 1052 (GOET).
French Guiana: Montsinéri, Leprieur 72 in part (FI, G, L), 167 (FI, G, NY); Mana, Perrottet s.n. (G); without loc., Leprieur s.n. (B, F, FI, K, L, NY).
Brazil. Amazonas: Bella Vista, R. Uaupés, Baldwin 3544 (US).
Amapá: Cunani, Huber 1110 (G).
Pará: Barra do Rio Tapajoz near Santarem, Spruce 931 (B, BM, C, G, GH, GOET, K, L, LE, NY, US, W).
Maranhão: Without loc., G. Don 142 (BR).
Pernambuco: Malti da Caxanga, Ridley, Lea & Ramage s.n. (BM); Malti da Iguarassa, id. s.n. (B, BM).
Bahia: Ilheos, Riedel s.n. (LE, NY); Marians, Riedel s.n. (L, LE).
Rio de Janeiro: Near Nova Friburgo, Beyrich s.n. (L); near Rio, Beyrich 1 (GOET); ibid., Chamisso s.n. (LE).
Perú. San Martín: Pacasmayo–Moyobamba, Stübel 1061 (B).

A specimen labelled „Panama" from R. W. Rawson's herb. in BM; specimens collected by L'Herminier said to have come from Guadeloupe in BM and G, this locality probably incorrect, never again found on that island.

Generally var. *parvula* can easily be separated from var. *stricta*, especially in the Guianas and Trinidad. There are, however, a few specimens which, though in size and shape of pinnules much like var. *parvula*, have only traces of the rachis-ridges or none at all which characterize that variety, and can be said to be intermediates between the two varieties. Because of their existance *L. parvula* Fée is reduced here to a variety. The following intermediates may be cited:

Venezuela. Amazonas: Maroa, R. Guainía, Ll. Williams 14331 a (US); Yavita, id. 13902 (F, US), 14065 (F, GH, US); La Esmeralda, Croizat 123 (MO, U).
Bolívar: Cerro Guaiquínima, Upper R. Paragua, Cardona 949 (US).
Brazil. Amazonas: Içana, Pirauána, von Lützelburg 22692 (M, NY, UC).
Piaui: Boqueirão near São João do Piaui, von Lützelburg 226 (M, US).
Bahia: Moritiba, Blanchet 3471 (BR, C, G, W); Marians, Riedel s.n. (B, GH, L, S–PA).

They are mostly restricted to the Amazon region, and their total number, as compared with that of typical specimens of var. *parvula*, is small.

c. var **jamesoniiformis** Kramer, var. nov. **Fig. 76**

Lamina percoriacea, pinnata vel bipinnata, pinnis valde adscendentibus, rhachide primaria laminae simpliciter pinnatae et rhachidibus secundariis facie abaxiali usque ad basin constanter angularibus, pinnulis rigidis, rotundatis, longitudine latitudinem sesquies vel minus superante, approximatis vel laxe imbricatis (interdum infimis exceptis), soris margine pinnularum recurvata saepe obtectis.

Typus: Maguire 24377 from Tafelberg, Suriname (US).

Petioles 5–54 cm long, from about half (rarely less) as long to more than 3 as long as the lamina, $^2/_3$–1½(–2) mm in diam. near the apex, dark red to black, dull, abaxially terete or with short lateral ridges at the extreme apex. *Lamina* once or twice pinnate, very coriaceous and rigid, medium green to dark greenish-brown, greyish or blackish, dull or slightly lustrous, ca. 10–35 cm long, linear when simply pinnate, otherwise with one odd to 3 (rarely to 5) pinnae to a side and a conform terminal one. *Primary rachis* of bipinnate leaves abaxially terete or angular above, of simply pinnate leaves as the secondary rachises of bipinnate ones. Axillary cushions not seen. *Pinnae* subopposite or almost so, strongly ascending (less so in plurijugate leaves), 5–20 cm long, ca. 3?4–1½ cm wide, widest at or slightly above the base, gradually narrowed to the apex, subsessile or the terminal short-stalked, the terminal by far the longest in paucijugate leaves. Secondary rachises (and primary rachis of simply pinnate leaves) red to blackish, abaxially laterally sharply angled, the angles extending almost to the base (or to the upper part of the petiole in simply pinnate leaves), the surface between them convex towards the base (and then sometimes almost conceiling the lateral angles) or for the greater part flattened. Rachis of terminal pinna abaxially often terete in a considerable basal portion. *Pinnules* ca. 30–100 to a side, close to slightly imbricate (succubous) or a few basal ones more remote, spreading or rarely slightly deflexed, mostly alternate throughout, roundish or occasionally slightly falcate, from 3 × 2 — 7 × 5 mm, a slightly reduced axillary pinnule mostly present. Inner margin slightly convex, touching or overlying the rachis, lower base shortly cuneate, hardly stalk-like, upper base rounded, lower margin shallowly S-shaped, the concavity mostly shallow, upper margin ± evenly convex, apex broadly rounded. Marginal thickening stramineous to medium brown, distinct throughout, entire or minutely repand along the upper/outer margin; margin of sterile pinnules entire or shallowly crenate in leaves of juvenile rhizomes. Terminal pinnule roundish, fertile along the distal edge. Sporangia ca. 215 × 165 μ; annulus with 10–12 indurated cells (fig. 21); indusium strongly reflexed at full maturity; sori often conceiled by the incurved margin.

Distribution: Northern South America (mostly Guayana) and Puerto Rico (map 33). In thickets and open forests or on exposed rocks (mostly sandstone), from ca. 1000–2300 m.

Vern. name: ari-epana-ú (Venezuela, Steyermark).

Puerto Rico: Sierra de Luquillo, Sintenis 1398 (B, BM, GH, GOET, K, L, LE, M, NY, S-PA, US); ibid., P. Wilson 96 (NY, US); ibid., Blauner 299 (B, BM, G); Mt. El Yunque, Sargent 307 (US); without loc., Schwanecke s.n. (B, GH); Palacky s.n. (W).

Colombia. Magdalena: Santa Marta, Purdie s.n. (NY).

Santander: Mesa de los Santos, Killip & A. C. Smith 15035 in part (US).

Venezuela. Amazonas: Cerro Yavé, Phelps & Hitchcock 9 (NY, US); Mt. Duida, summit, Tate 777 (NY); ibid., Steyermark 58246, 58282 (F, MO, NY, US).

Bolívar: Auyan-tepuí, Tate 1269 (NY); Uaipan-tepuí, Phelps & Hitchcock 374 (NY); Ptari-tepuí, Steyermark 59502 (F, US), 59735 (F, MO, NY, US); Chimantá-Massif, summit of Abácapa-tepuí, Steyermark 74846 (US); Gran Sabana, Steyermark 58576 (F, NY, US).

British Guiana: Kaieteur Savanna, Jenman s.n. (NY); ibid., Sandwith 1284 (BM, K, U); ibid., Jenman 1387 (K); ibid., Im Thurn s.n. (K); Kaieteur plateau, Maguire & Fanshawe 23159 (A, F, G, K, MO, NY, U, UC, US); Potaro R., Santini s.n. (L); Mt. Roraima, McConnell & Quelch 76 (BM); ibid., Im Thurn 149, 150 (BM, K, US); ibid., summit‘ McConnell & Quelch 497, 557 (K); without loc., Jenman s.n. (US).

SURINAME: Tafelberg, Maguire 24377 (US, HOLOTYPE; Isotypes in A, F, G, K, MO, NY, S–PA, U, UC).

The combination of very coriaceous pinnules, strongly ascending pinnae, dark axes, and abaxially angular rachises of the highest order characterize this variety very well, although these characters occur also in other varieties of *L. stricta*, but not together. Var. *jamesoniiformis* is, as a whole, very clear-cut and could perhaps be raised to subspecific or specific rank, but it is very close to typical *L. stricta*; intermediates have hardly been found, not even in the few localities where both varieties occur side by side (Santa Marta, Mt. Roraima). Simply pinnate leaves and pinnae of paucijugate bipinnate ones resemble a species of the genus *Jamesonia;* the specimens from Puerto Rico are smaller, not unlike *Polypodium moniliforme* Lag.

The closest relative of *L. stricta* is *L. portoricensis;* the differences are discussed under that species. *L. javitensis* is also allied (see there). *L. pallida* is sometimes confused with *L. stricta;* it has more strongly erose indusia, sori not covered by the reflexed margin, and monolete spores.

28. **Lindsaea javitensis** Humboldt & Bonpland ex Willdenow, Sp. Pl. V:424 (1810); Poiret in Lamarck, Encycl. Suppl. III:448 (1813); Kunth in H. B.K., Nov. Gen. & Spec. I:18 (1815); Desvaux, Prodr. 313 (1827); Sprengel, Syst. Veget. IV: 80 (1827); Presl, Tent. Pterid. 131 (1836); not of Raddi, Plant. Bras. Nov. Gen. 56 (1825). **Fig. 66, 67**

Type: Humboldt & Bonpland s.n. from Yavita, Venezuela (Willdenow-herbarium in B, not seen; photographs in BM and U!).

Misapplied name: *L. stricta* of Hooker, Spec. Fil. I:216 (1844), in part, non Dryand.

Petioles reddish brown, abaxially terete; lamina bipinnate with conform terminal pinna, coriaceous; secondary rachises abaxially angular; pinnules subovate to tongue-shaped, almost 2 × as long as wide, the upper ones gradually and strongly reduced; veins immersed or slightly elevated; sori continuous; indusium irregularly repand-erose; spores trilete.

Rhizome creeping, ca. 4 mm in diam.; scales pale castaneous, shining, lanceolate, long-acuminate, up to 2 mm long and 0.4 mm wide, with up to 10 rows of cells at the base. *Petioles* close, (15–)25–50 cm long, 1.5–2 mm in diam. near the apex, of a very characteristic reddish-brown colour suffused with purple, darker at the extreme base, rather glossy, terete, only the upper part of the adaxial surface flattened to shallowly sulcate, the borders not sharp. *Lamina* roughly as long as the petiole, yellowish to brownish green, with 6–15 pinnae to a side and a conform terminal one; lateral pinnae subopposite, or the upper ones (rarely all) alternate, 3–5 cm apart, or the upper ones closer, patent under an angle of ca. 30–50°, short-stalked, the lateral a few mm, the terminal up to 1 cm; lower pinnae about 10–15 cm long, 1–1.5 cm wide, the terminal longer than the slightly reduced upper lateral ones. *Primary rachis* similar to the upper part of the petiole. Upper half or two-thirds of the pinnae very gradually narrowed, the apex thus acuminate, the base shortly narrowed. Secondary rachises flattened abaxially and adaxially, with sharp borders, shallowly sulcate towards the apex, only a short basal portion terete on the abaxial side. *Pinnules* ca. 35 to 50 to a side, subopposite to alternate, spreading or slightly ascending, a few somewhat reduced ones at the base, a strongly reduced axillary one sometimes present, rather close and regularly spaced but not contiguous, 5–7 mm long, 2.5–4 mm wide. Inner margin straight, parallel, often touching the rachis, upper edge rounded, especially towards the apex, where it gradually passes into the straight lower margin; upper base rounded, lower base hardly stalk-like. All edges, also in sterile pinnules, entire. Marginal thickening strong and conspicuous along the lower edge, otherwise slightly weaker, pale brown. Veins on both surfaces elevated near their bases, sometimes inconspicuously raised throughout, not stramineous, simple or once forked, ca. ½–¾ mm apart at the margin; main vein for ¼ or ⅓ of its length united with the marginal strand, for the rest slightly divergent from it. Upper pinnules gradually and strongly reduced, the uppermost about 1 mm long, but hardly confluent, with a slightly larger (2–3 mm), almost free terminal segment with blunt apex. *Sori* along the upper/outer margin; indusium rigid, ca. 0.2 mm wide, almost equalling the margin, ± reflexed at full maturity. Sporangia 200–205 × 160 μ; annulus with 10–13 indurated cells; spores rather pale brown, ca. 32–40 μ.

Distribution: North-western South America; apparently uncommon (map 30). On campos and savannas, in gravel and among boulders in sandy soil, up to 250 m.

COLOMBIA. VAUPÉS: Río Kananarí, trib. of R. Apaporis, Cerro Isibukuri, Schultes & Cabrera 14528 (US).

AMAZONAS–VAUPÉS: Cachivera de Jirijirimo, R. Apaporis, Schultes & Cabrera 12965 (US).

VENEZUELA. AMAZONAS: Yavita, Humboldt & Bonpland s.n. (Type, herb. Willdenow in B, not seen; photographs in BM and U); "Caracas", prob. incorrect, without coll. or number (S–PA).

BRITISH GUIANA: Amatuk Portage, Potaro R., Sandwith 1255 A in part (K; juv.).

BRAZIL. AMAZONAS: Rio Negro, São Felippe, von Lützelburg 22605 (NY, UC); ibid., id. 22387 (M, UC); Rio Negro, Tapacal, von Lützelburg 22902 (M, UC).

Probably most closely allied to *L. rigidiuscula*, which differs by larger pinnules and abaxially sharply angular petiole; also to *L. stricta*, which has more strongly immersed veins, fewer, more strongly ascending pinnae (except in the herbaceous, mainly, s.e. Brazilian form), and upper margins often incurved around the sorus. The three species agree in their small, rigid pinnules, which is in accordance with their preference for open habitats. *L. javitensis* was incorrectly referred to *L. guianensis* by Christensen (Ind. Fil. p. 394).

29. **Lindsaea rigidiuscula** Lindman, Hedwigia 43:308 (1904); Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930). **Fig. 68**

Type: without collector or number, said to be from Caracas, Venezuela (S-PA!).

Homotypic synonym: *L. nervosa* Lindman, Ark. f. Bot. 1:199 (1903) pl. 8 fig. 5, non Mettenius, 1861.

Petioles dull olivaceous with paler angles, quadrangular; lamina bipinnate with conform terminal pinna, chartaceous; primary and secondary rachises abaxially angular; pinnules semi-ovate or subfalcate, ca. 2½ × as long as wide, the upper ones gradually reduced; veins elevated; terminal pinnule distinct but small; sori continuous; indusium subentire or slightly repand; spores trilete.

Rhizome creeping, 2–3 mm in diam.; scales lanceolate, long-acuminate, up to 1¾ cm long, 0.3 mm wide, with up to 9 rows of cells at the base. *Petioles* close, 6–43 cm long, from half as long as to slightly longer than the lamina, 1–2 mm in diam. at base of lamina, a short basal portion (a few cm) terete, otherwise quadrangular. *Lamina* brownish to yellowish green, with 1–8 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole. Axillary cushions present, inconspicuous. *Pinnae* subopposite or the upper ones alternate, the lower 3–7 cm apart, the upper closer, short-stalked (up to 8 mm) to sessile, forming an angle of 30–45° (rarely more) with the primary rachis, up to 30 cm long, the upper ones much shorter in plurijugate leaves, up to only 5 cm long, 15–37 mm wide, mostly ca. 20–30 mm, very shortly narrowed at the base, the upper two-thirds very gradually tapering to the apex. Secondary rachises abaxially terete at the extreme base, otherwise angular, adaxially with a narrow dark or reddish brown channel bordered by stramineous ridges. *Pinnules* 15 to 50 to a side, subopposite or alternate, spreading or, especially the upper ones, laxly ascending, never decurved, the larger ones 9–17 × 4–8 mm, subsessile, 1–3 basal ones on each side reduced, a strongly reduced axillary pinnule usually present. Inner margin ± parallel to the sec. rachis, often touching it, lower margin substraight or concave, upper margin rather strongly convex, especially towards the apex which is subacute, rounded in sterile or incompletely fertile pinnules. Margins entire in fertile pinnules, very shallowly crenate in sterile ones, the incisions not over 0.4 mm deep, the lobes uni- or binerval, rounded or subacute. Marginal strand narrow and stramineous except at the base of the lower edge where it is thick and often reddish. Veins very close, 0.5–0.75 mm apart at the margin, conspicuously elevated on both surfaces, stramineous to pale green, two to three times forked; the pinnules are stiff through the close veins and indurated margin. Upper pinnules gradually reduced, but not confluent; terminal pinnule always distinct, oblong-lanceolate, obtuse, mostly lobed at the base, 5–10 mm long, often soriferous. *Sori* along the upper/outer margin. Indusium rigid, ca. 0.2 mm wide, not reaching the margin by a distance equalling its width, reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ; annulus with 10–13 indurated cells; spores medium brown, ca. 34 × 30 μ.

Distribution: Northern South America; apparently uncommon (map 36). On campos, glades, and forest clearings and in light secondary forest, often on sand, up to 130 m.

COLOMBIA. VAUPÉS: Río Kananarí, Cerro Isibukuri, Schultes & Cabrera 15070 (US).
VENEZUELA. AMAZONAS: Maroa, Río Guainía, Ll. Williams 14329 (F, GH, US); ibid., id. 14263 (F, US); Yavita, Upper Atabapo, Ll. Williams 16126 (US). "Caracas", probably coll. in southern Venezuela, without collector or number (S–PA, HOLOTYPE; fragment in C. Chr. in BM).
BRAZIL. AMAZONAS: R. Uaupés, Iutica, von Lützelburg 23601 (M); Tunuy, R. Içana, Koch 65 (B).
GOIAS: Sucuriu on Rio das Femeas, von Lützelburg 1509 in part (UC).

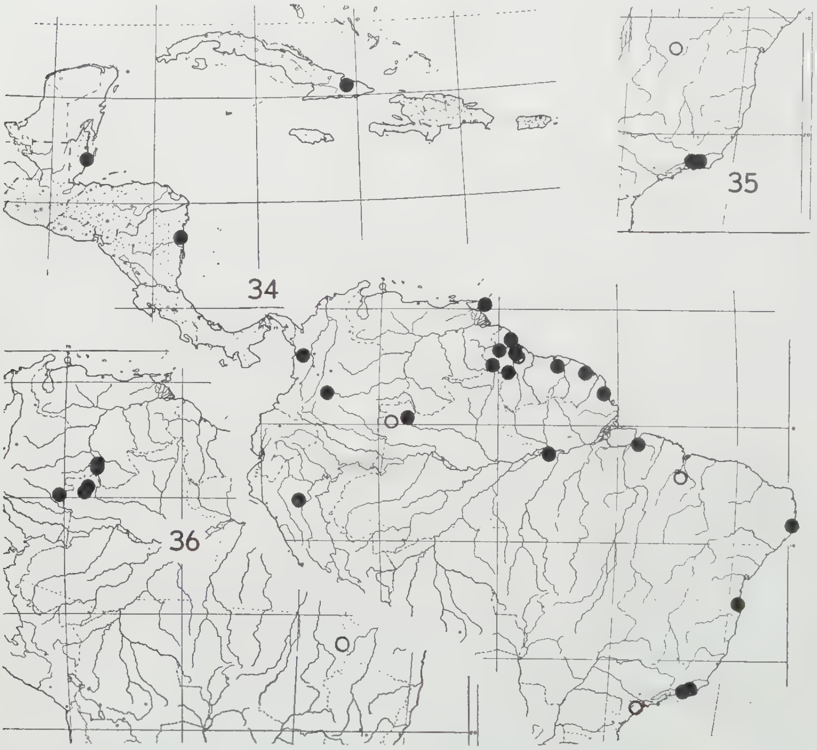
The combination of rigid pinnules with raised veins and abaxially angular axes serves to distinguish this species easily. Its closest relative seems to be *L. javitensis;* the differences are discussed under that species. It is unlikely that the type was collected near Caracas, as it was never found again in that vicinity, and all other collections are from the Guianan or Brazilian shields.

30. **Lindsaea filipendula** (Rosenstock) Kramer, comb. nov. **Fig. 72**

Basionym: *L. guianensis* (lapsu: *gnianensis*) (Aubl.) Dryand. var. *filipendula* Rosenstock, Fedde Rep. 20:93 (1924); *L. filipendula* Ros., ibid., nom. provis.

Lectotype: von Lützelburg 141 from Sucuriu, Rio das Femeas, Goias, Brazil (M!).

Petioles reddish brown to blackish, very delicate, wiry; lamina simply pinnate, bipinnate with conform terminal pinna, or rarely subtripinnate, herbaceous; pinnules dimidiate-ovate to dimidiate-elliptic or subtriangular, ca. 1½ × as long as wide, the upper ones gradually reduced; upper/outer margin conspicuously and very irregularly erose-lacerate in fertile pinnules; sori continuous; indusium very wide, equalling or surpassing the margin, irregularly lacerate; spores trilete.



Map 34: *L. stricta* var. *parvula*. Map 35: *L. filipendula*. Map 36: *L. rigidiuscula*.

Rhizome short-creeping, slender, 1 mm in diam.; scales ovate to broadly lanceolate, acute or shortly acuminate, minute, up to 0.7 mm long and 0.3 mm wide, with up to 9 rows of cells at the base (fig. 4). *Petioles* close, 8–20 cm long, ½–⅔ as long as the lamina, diam. 0.3–0.6 mm, dull, subterete at the base the upper part abaxially obtusely angular or terete, adaxially flattened, with sharp borders, shallowly sulcate towards the apex. *Lamina* up to 25 cm long, pale green to brown. *Primary rachis* similar to the upper part of the petiole but often paler, esp. above. Axillary cushions not visible. *Pinnae* (if any) 1–5 to a side and a conform terminal one, the lower ones (and simply pinnate laminae) 10–15 cm long, 1–1.5(–2) cm wide; lateral pinnae somewhat decurrent, subopposite or alternate, short-stalked to subsessile, laxly spreading under an angle of 40–50°, rather widely spaced, 2–3 cm apart, the upper ones closer and shorter, sometimes considerably reduced, terminal pinna mostly distinctly stalked, longer than the lateral ones. Secondary rachises abaxially stramineous to pale brown, with a sudden transition from the darker colour of the primary rachis at the point of insertion, in the terminal pinna more gradual, terete, adaxially with a narrow groove, concolorous with the primary rachis. *Pinnules* ca. 20–35 to a side, mostly alternate throughout, the larger ones rather constant in size, 6–7 mm long, 4–5 mm wide, widest at the base, the basal ones hardly reduced, even the axillary one which is invariably present but little reduced but somewhat adnate, the other pinnules short-stalked, more or less spreading, the lower ones their width or more apart, the upper ones closer but not contiguous. Inner margin ± straight, mostly touching or slightly overlying the sec. rachis, upper base shortly rounded, lower base long-cuneate, lower margin convex, upper margin slightly and evenly convex, conspicuously and very irregularly erose-lacerate in fertile pinnules, superficially crenate or sinuous to subentire in sterile ones, this difference even observed between sterile and fertile parts of the upper margin of a single pinnule; apex broadly rounded, no outer margin developed. Marginal thickening not conspicuous but evident, stramineous to pale reddish, virtually absent in the lacerate upper margin of fertile pinnules. Veins once or the basal one twice forked, immersed, ¾–1 mm apart at the margin; main vein distinctly intramarginal, ca. ½ mm above the lower margin near the apex. Upper pinnules (in the upper $^2/_3$ or more or the pinna) gradually reduced, the uppermost ones ca. 2–5 mm long, confluent into a lobed spathulate often soriferous terminal segment. *Sori* along the upper margin; indusium 1–1.5 mm wide, very irregularly and (under the lens) conspicuously lacerate, sometimes cleft, in addition often plicate, pale, often with reddish margin, not reflexed at maturity. Sporangia 210–220 × 150 μ; annulus with 11–14 indurated cells; spores almost globose, medium to dark brown, ca. 32 μ, 32?

Distribution: Eastern Brazil (map 35). No ecological data extant.

BRAZIL. GOIAS: Sucuriu on Rio das Femeas, von Lützelburg 141 (M, LECTOTYPE; Isotypes in NY, UC).

RIO DE JANEIRO: Serra d'Estrella, Cortisso, von Lützelburg 252 (C, M, NY, UC, US, W, Paratypes); Serra dos Orgãos, Morro Assú, von Lützelburg 13751 (M, Paratype).

Not at all close to *L. guianensis* and generally of doubtful alliance among the American species; possibly distantly related to *L. stricta* or *L. ovoidea*, perhaps to *L. tenuis* with which it shares the wiry axes and the minute broad scales. The very delicate axes and the extremely wide, lacerate indusia are most distinctive.

31. **Lindsaea tenuis** Klotzsch, Linnaea 18:550 (1844); Hooker, Spec. Fil. I:218 (1844); Baker, Fl. Bras. I²:353 (1870); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 79 (1899); Diels, N. Pfl. I⁴:221 (1902); Posthumus, Fl. Surin. Suppl. 72 (1928). **Fig. 28**

Type: Schomburgk 1185 from British Guiana (B!).

Heteroptypic synonym: *Lindsaea filiformis* Hooker, Spec. Fil. I:218 (1844): Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 106. Type: Schomburgk 1185 from Mt. Roraima, British Guiana (K!).

Petioles dark, very delicate, wiry; primary rachis similar, flexuose; lamina bipinnate with conform terminal pinna, chartaceous; pinnules obliquely triangular, ca. 2 × as long as wide, not over 6 × 3 mm, the upper ones somewhat reduced, the terminal segment sometimes distinct; sori continuous; indusium rather wide, minutely erose to laciniate, about equalling the margin; spores trilete.

Rhizome creeping (short?), delicate, ca. ¾ mm in diam.; scales minute, ovate, obtuse, acute, or apiculate, up to 0.35 mm long and 0.2 mm wide, with up to 4 rows of cells at the base. *Petioles* 5–12 cm long, much shorter than the lamina, 0.4–0.5 mm in diam., shining, subterete except for the upper part of the adaxial side which has a flattened portion with sharp paler borders, the surface between them somewhat sunken. *Lamina* bipinnate (very rarely simply pinnate), ca. 10–85 cm long, 4–10 cm wide, medium to brownish green, with 4–? pinnae to a side and a conform terminal one. Axillary cushions not seen. Pinnae in subopposite pairs, the members of a pair up to 1(–2) cm apart, the lower pairs in large leaves very remote, up to 12 cm apart, the upper ones gradually closer; mostly laxly ascending, forming with the primary rachis an angle of ca. 45°, subsessile to short-stalked (–7 mm), 3.5–6 cm long, 1–1.5 cm wide, mostly not strongly narrowed to the apex, often narrowed at the base. Secondary rachises similar to the primary but paler in their upper part, mostly reddish, ca. 0.2 mm in diam. *Pinnules* 7–13 to a side (in the terminal pinna of paucijugate leaves, which is the largest, up to 35), alternate, subsessile, not close, separated by spaces approximately equal to their width, never contiguous, the largest 4–6 mm long, 2–3 mm wide, narrowed-obtuse at the apex. Lower base with a short stalk-like base, inner margin convex, divergent from the sec. rachis, upper base obtuse, lower margin straight or slightly convex, upper margin subentire or in some of the sterile pinnules crenate, in addition mostly minutely erose. Marginal thickening obsolete except at the base of the lower margin where it is reddish. Veins immersed, hidden, simple or once forked, their ends 1–1.5 mm apart; small pinnules with only 2 veins. Lower pinnules sometimes very gradually reduced, the basal ones then minute; upper pinnules somewhat, but not very strongly, reduced, one of them sometimes connected by a wing with the terminal segment (pinnule) which is about the same size as one of the larger lateral ones, asymmetric, lanceolate, soriferous. *Sori* along the upper margin; indusium ca. 0.5 mm wide, ± reflexed at full maturity. Sporangia ca. 170 × 120 μ; annulus with 9–10 indurated cells; spores pale brown, ca. 26–31 μ.

Distribution: Venezuela and British Guiana; apparently extremely rare (map 26).

VENEZUELA. BOLÍVAR: Lower slopes of Carrao-tepuí; climbing, appressed to mossy tree-trunks; woods, 1675–1980 m; Steyermark 60959 (F, K, MO, NY, US). BRITISH GUIANA: Roraima, Schomburgk 18 (BM); without loc., prob. ibid., Schomburgk 1185 (B, HOLOTYPE; BR; K, HOLOTYPE of *L. filiformis*).

The elongate, flexuose, wiry rachis is unique among the neotropical species and perhaps in the whole genus. The only species to which it is perhaps allied is *L. filipendula*.

Subsectio 3. **Terminales** Kramer, subsect. nov.

Pinnulae fertiles ut in subsectione *Decrescentes*, sed superiores paullum vel paene decrescentes, pinnula terminalis magna, libera. Lamina in speciebus omnibus interdum, in nonnullis semper simpliciter pinnata.

Species typica: *Lindsaea lancea* (L.) Bedd.

As has been pointed out above (p. 138), it is not certain whether this subsection is a phyletic entity, as it may have been developed from subsection *Decrescentes* along several lines. For this there is, however, no conclusive evidence.

32. **Lindsaea lancea** (L.) Beddome, Ferns Brit. India Suppl. 6 (1876); Kuhn, Chaetopt. 26 (1882); Christ. Farnkr. d. E. 292 (1897), as to New World specimens only; Krug in Urban, Engl. Bot. Jb. 24:91 (1897); Diels, N. Pfl. I^4:221 (1902), as to New World specimens only; Kuhn in Urban, Symb. Ant. 4:30 (1903); Lindman, Ark. f. Bot. 1:198 (1903); not pl. 8 fig. 2 and 3; Rosenstock, Hedwigia 46:79 (1906); Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. II:150 (1915), VII:374 (1918); Hieronymus, Hedwigia 62:14 (1920); Urban, Symb. Ant. 9:321 (1925); Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Maxon, Pterid. Port. 490 (1926);

Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928), in part; Posthumus, Fl. Surin. Suppl. 75 (1928); Domin, Pterid. Domin. 244 (1929); Sampaio, Arch Mus. Nac. Rio de Jan. 32:35 (1930), pl. 12 fig. 1, 2, 4; Standley & Record, Field Mus. Publ. 350:64 (1936); Christensen, Kungl. Sv. Vet.-Ak. Handl. 3e Ser. 16 (2):46 (1937); Stehlé, Caribb. For. 4 (2): 92 (1943); Dutra, An. Prim. Reun. S.—Am. Bot. 2:29 (1938); Capurro, ibid.: 106 (1938); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948); Hodge, Lloydia 17 (2): 102 (1954).

Basionym: *Adiantum lancea* L., Spec. Pl. ed. 2, II:1557 (1763); Willdenow, Spec. Pl. V:440 (1810); Poiret in Lamarck, Encycl. Suppl. I:136 (1810); not of Baker, Fl. Bras. I²:373 (1870).

Type: no specimen extant (see below).

Homotypic synonym: *Lindsaea falcata* Dryand. var. *lancea* (L.) Jenman, W. Ind. Gui. F. 74 (1899).

Heterotypic synonyms: *L. trapeziformis* Dryander, Trans. Linn. Soc. 3:43 (1797) pl. 9; Roem. Arch. 2 (II):236 (1801), t. IV fig. 4; Swartz, Syn. Fil. 119 (1806); Willdenow, Spec. Pl. V:424 (1810); Sprengel, Syst. Veg. IV:79 (1827); Desvaux, Prod. 313 (1827); Kunze, Linnaea 9:87 (1835); Presl, Tent. Pterid. 131 (1836); J. Smith, Lond. Jo. Bot. 1:200 (1842); Hooker, Spec. Fil. I:214 (1844), in part; Klotzsch, Linnaea 18:546 (1844); Kunze, Linnaea 21:226 (1848); Bot. Zeit. 8:348 (1850); J. Smith in Seemann, Bot. Voy. Herald 239 (1854); Ettingshausen, Farnkr. 212 (1865), in part, t. 146, fig. 4, 5; Fée, 11e mém. 15 (1866); Grisebach, Catal. Plant. Cub. 274 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 107, excl. of almost all synon.; Fée, Crypt. vasc. Brés. I:29 (1869); Baker, Fl. Bras. I²:355 (1870), in part, excl. of most synon. and var., t. 41 fig. 5; J. Smith, Hist. Fil. 268 (1875); Eaton, Bot. Gaz. 3 (11): 89 (1878); Britton, Bull. Torr. Bot. Cl. 15:248 (1888); Sodiro, Crypt. Vasc. Quit. 56 (1893); Bommer & Christ, Prim. Fl. Costar. (Bull. Soc. Roy. Bot. Belg. 35): 115 (1896); Shimek, Ferns Nicar. 151 (1897), pl. XI fig. 1, 4, 5, 6, 7; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. min.; Rosenstock, Hedwigia 43:216 (1904), in part; Duss, Fl. Crypt. Ant. franç. 58 (1904), p.p. mai. Type: Smeathman s.n. from Grenada (not seen).

L. nitidissima Richard ex Willdenow, Spec. Pl. V:423 (1810); Poiret in Lamarck, Encycl. Suppl. III:447 (1813); Presl, Tent. Pterid. 131 (1836); Klotzsch, Linnaea 14:287 (1840); Alston Kew Bull. 1932: 311. Type: unknown coll., "habitat in Gujana (v.s.)", in herb. Willdenow (B, not seen; photograph in U!).

Pteris adiantoides Vellozo, Fl. Flumin. 11 t. 88 (1827), teste C. Christensen, Ind. Fil. 591 (1906), non Bory, 1810.

L. imbricata Liebmann, Vid. Selsk. Skr. 5 (1): 269 (1849), non Devaux, 1811. Type: Liebmann 2447 from San Pedro Tepinapa, Oaxaca, Mexico (C!).

L. lancea (L.) Bedd. var. *subtripinnata* Rosenstock, Hedwigia 46:79 (1906). Type: Goeden 22 from Blumenau, Santa Catarina, Brazil (UC!).

L. Abbottii Brause, Fedde Rep. 18:245 (1922); Urban, Symb. Ant. 9:322 (1925). Type: Abbott 824 from Cotuy, San Domingo, Hispaniola (US!).

Misapplied names: *L. montana* auct. non Fée; Urban, Symb. Ant. 9:322 (1925).

L. schomburgkii of Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. mai.

Petioles pale or dark, abaxially angular or rounded; lamina simply pinnate or bipinnate with conform terminal pinna, herbaceous; pinnules subtrapeziform to subfalcate of falcate, angular at the apex, up to 3 × as long as wide; upper pinnules somewhat or hardly reduced, terminal pinnule quite free, large, triangular-lanceolate; sori continuous; indusium rather narrow, mostly entire; spores trilete.

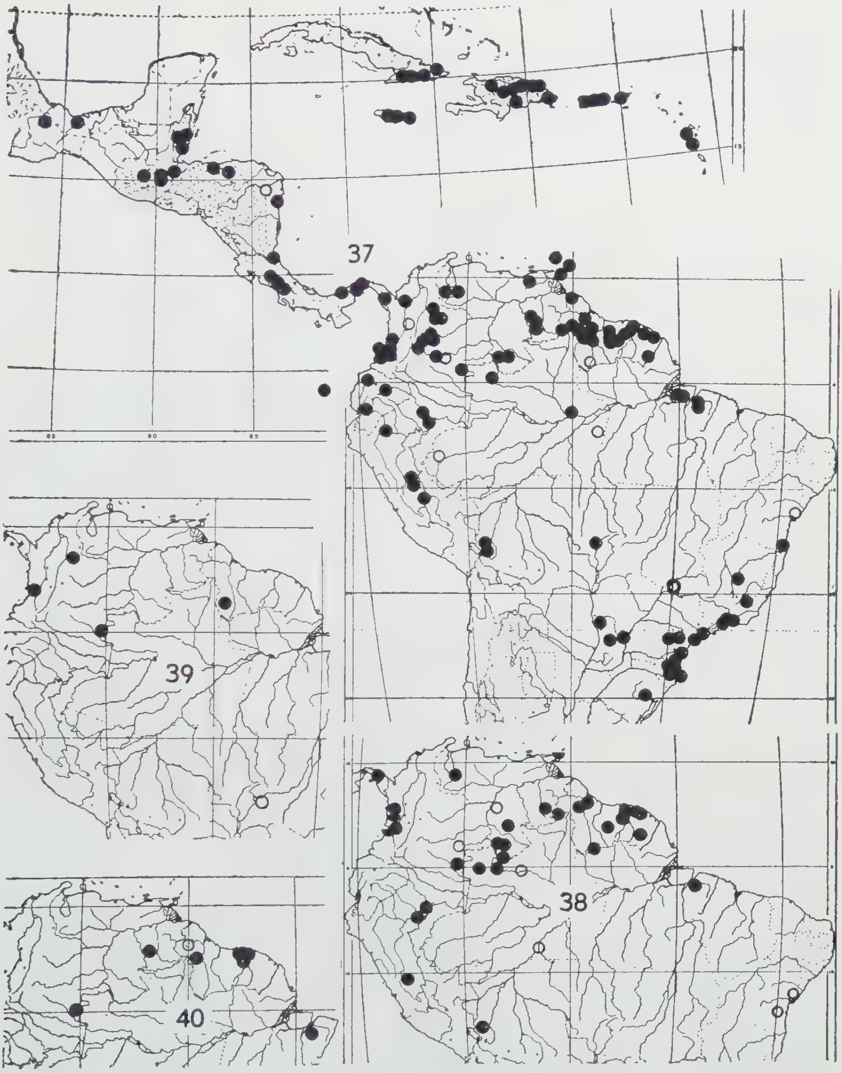
This very polymorphous species consists of five more or less distinct varieties, which can be distinguished as follows:

1. a. Terminal pinnule very obtuse; leaves simply pinnate, with numerous pinnules, the upper ones gradually and rather strongly reduced . . . . c. var. *elatior*
   b. Terminal pinnule acute or subacute; leaves bipinnate, or, if simply pinnate, the upper pinnules but little reduced . . . 2
2. a. Pinnules small, 10–16 mm long, 5–8 mm wide, gradually narrowed to the apex which is mostly subacute; a distinct outer margin mostly not developed . . . .b. var. *remota*
   b. Pinnules 11–45 mm long, 6–20 mm wide, mostly of equal width close to the apex, which is ± rectangular, or, if subacute, points obliquely downwards; a distinct outer margin mostly present 3
3. a. Pinnules about 2–2½ × as long as wide, 11–37 mm long, 6–14 mm wide, the upper ones about half as long as the lower ones; terminal pinnule longer than wide, or, if as long as wide, not very asymmetrical; pinnate or bipinnate a. var. *lancea*
   b. Pinnules up to 3 × as long as wide, up to 45 mm long and 20 mm wide, the upper ones little or not reduced; terminal pinnule about as long as wide, very asymmetrical . . . 4
4. a. Petiole reddish-brown to blackish, abaxially in at least about the upper half with pale, slightly wing-like angles d. var. *falcata*
   b. Petiole black, abaxially terete throughout or angular at the extreme apex only . . . . e. var. *leprieurii*

a. var. **lancea.** **Fig. 79**

Misapplied names: *L. falcata* auct. non Dryand.; Krug in Urban, Engl. Bot. Jb. 24:91 (1897); Jenman, W. Ind. Gui. F. 74 (1899), in part; Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. mai.; Graham, Ann. Carnegie Mus. 22:87 (1934); Standley & Record, Field Mus. Publ. 350:64 (1936); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948), in part; Alston, Mutisia 7:6 (1952).

L. trapeziformis Dryand. var. *falcata* Baker of Eaton, Bot. Gaz. 3



Maps 37–40: *L. lancea;* map 37: var. *lancea;* map 38: complete dots: var. *falcata;* half dots: intermediates between var. *falcata* and var. *lancea;* map 39: var. *elatior;* map 40: var. *remota.*

(11):91 (1878), not *L. falcata* Dryand.
L. lancea (L.) Bedd. var. *falcata* Rosenstock, Hedwigia 46:79 (1906), as to specimen cited, not *L. falcata* Dryand.

This variety, the most variable of the species, consists of two extreme forms, which, although they are connected by a large number of intermediates, can best be described separately in order to avoid too many alternatives in the descriptions.

The bipinnate form.

Rhizome creeping, mostly with several short lateral branches, sometimes long-creeping, rather stout, 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2 mm long, 0.2 mm wide, with up to 8 rows of cells at the base. *Petioles* close, ca. 10–50 cm long, mostly about as long as the lamina, not infrequently up to 1½ × as long or more, 1–1.5(–2) mm in diam. near the apex, dark brown at the base, for the rest stramineous or pale brown, rarely raddish or olivaceous-brown throughout, then above with paler angles, more or less shining, adaxially sharply angular almost to the base, the surface flat or, especially above, sulcate, abaxially sharply angular almost to the base or sometimes below obtusely angular or subterete. *Lamina* mostly bipinnate (very rarely subtripinnate; this form was described as a variety by Rosenstock but can hardly be kept apart), dark green on the ventral, dark or medium green on the dorsal side, herbaceous, 11–52 cm long, with 1–8, mostly 3 or 4 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially at least above sulcate. Axillary cushions visible as swellings but usually not discoloured. *Pinnae* alternate or the lower subopposite, angle with the primary rachis rather variable but mostly ca. 45–60°, the lower ones ca. 3–7 cm apart, the upper ones in plurijugate leaves gradually closer, subsessile or short-stalked (the terminal often longer, up to 2 cm), lanceolate, 10–32 cm long, 1–5 cm wide, the upper ones in plurijugate leaves about $^{2}/_{3}$ as large as the lower ones, the terminal not smaller, widest around the middle or just above the base, slightly narrowed towards the base, more gradually but not strongly narrowed to the apex, not acuminate. Secondary rachises adaxially sulcate, abaxially terete at the extreme base, two ridges appearing abruptly at the level of the 1st–3rd pinnule which soon occupy a lateral position, the portion between them flat or mostly at least below sulcate, the ridges often paler, sometimes obscurely wing-like, merging into a keel in or just below the terminal pinnule. *Pinnules* ca. 12–35 to a side, alternate or sometimes subopposite, spreading or the upper ones laxly ascending, the basal ones occasionally decurved, rather close to contiguous or slightly overlapping, mostly subtrapezoidal, occasionally dimidiate-ovate or subfalcate, ca. 11–23(–29) mm long, 6–11 mm wide, mostly from slightly less than 2–2½ × as longas wide, equally wide from the base close to the apex, rarely more gradually narrowed. Inner margin straight, parallel to the sec. rachis or slightly divergent, lower base cuneate, hardly stalk-like, upper base shortly rounded, often subangular, upper margin almost straight, connected by a short convex portion with the substraight outer margin, rarely more evenly rounded, gradually passing into the outer margin, lower margin straight, sometimes faintly concave, or in basal pinnules more strongly so. Apex usually aproximately rectangular, less often obtuse or apiculate. Marginal thickening stramineous, inconspicuous but visible throughout, or indistinct along the soriferous margins. All margins entire in fertile pinnules, in sterile ones the upper and outer mostly shallowly sinuate or crenate, with incisions up to 1 mm deep, rarely quite entire. Veins immersed or the bases sometimes elevated, readily discernible, mostly twice forked, ca. ¾–1 mm apart at their ends, Main vein hardly connected with the marginal strand, ca. ½–¾ mm above it near the apex. Upper pinnules not strongly reduced, about $^{2}/_{3}$ or ½ the size of the lower ones. Terminal pinnule quite free, lanceolate, mostly broadly so or even triangular, asymmetrical at the often shallowly lobed base, obtuse or mostly acute, acuminate, or even caudate, ca. (10–)25–70 mm long, (4–)10–25 mm wide, at least 1½ × as long as wide, with a percurrent midrib, soriferous in the basal lobes, rarely throughout. *Sori* continuous along the upper and outer margin; indusium narrow, ca. 0.2–0.3 mm wide, entire, not reaching the margin by 2–4 times its own width, reflexed and conceiled at full maturity. Sporangia ca. 135 × 105 μ; annulus with 10–12 indurated cells; spores trilete, pale yellowish-brown, 22–25 μ, 32?

The simply pinnate form. (All characters not mentioned are as in the bipinnate form).

Rhizome 1.5–2.5 mm in diam.; *petioles* sometimes not very close, 7–22 cm long, half as long to as long as the lamina, mostly dark reddish-brown to atropurpureous, occasionally olivaceous or stramineous, the abaxial side usually terete below, sometimes close to the apex, the angles often distinctly wing-like in the upper part. *Lamina* 6–30 cm long, 2.5–6(–8) cm wide. *Rachis* with sharp or wing-like angles throughout. *Pinnules* ca. 7–25(–30) to a side, subopposite or alternate, spreading or slightly deflexed, the basal ones often more strongly so, up to 37 mm long (rarely) and 14 mm wide, often more falcate than in the bipinnate forms, with more acute apex. Terminal pinnule often long-acuminate. Indusium sometimes closer to the margin.

The pinnate form is more variable than the bipinnate form. The extremes look rather different, and it is not difficult to understand that the two forms were regarded as separate species for a long time; the simply pinnate form was included in *L. falcata.* Study of the very large number of specimens available at present shows, however, that such a distinction is artificial, even when additional characters such as colour and structure of the stipe are used. Both forms are sometimes found together on the same rhizome; they occur side by side in the same habitats almost throughout the range of the species. Generally the bipinnate form is more common; the simply pinnate form seems to be commonest in Trinidad. It has so far not been found in the West Indies, except Puerto Rico, Jamaica, and Grenada.

Distribution: Throughout the range of the genus in the New World (map 37). Common and often abundant. Mostly in forests, sometimes in thickets, palm-groves or in swamps, on sandy or clayey soil, occasionally on trunks of trees or on decaying logs, from sea-level to 1500 m (rarely at higher altitudes).

Vern. names: avenca (Pará, Brazil, Miles Moss); warakoewirie Suriname).

Representative or widely distributed specimens:

MEXICO. VERA CRUZ: Coatzacoalcos, Ch. L. Smith 2078 in part (GH, IA, UC). OAXACA: Tepinapa, Galeotti 6496 (BR, LE); San Pedro Tepinapa, Chimantla, Liebmann 2447 (C, HOLOTYPE of *L. imbricata*).

BRITISH HONDURAS: Mountain Pine Ridge, El Cayo Distr., Bartlett 11713 (F, MO, UC, US); Big Creek, Schipp 100 (B, BM, F, G, GH, K, NY, UC, US).

GUATEMALA: Cubilquitz, Alta Verapaz, von Türckheim II 27 (Donnell Smith-exs. 7707) (B, BR, S–PA, US); Izabal, near Puerto Barrios, Standley 25006 (NY, US); near Entre Rios, Standley 72761 (F, US).

HONDURAS: Lancetilla Valley, near Tela, Dept. Atlántida, Standley 53133 (F, US); near Ceiba, Dyer A 194 (US).

NICARAGUA: Karatá, Schramm 29 (S–PA); Sangsangta Distr., Schramm 38 (US); Camp Menocal near Greytown, Shimek s.n. (IA).

COSTA RICA: El General, Skutch 4127 (BM, GH, MO, NY, US); Buenos Aires, Kupper 1363 (M); Cocos Island, Pittier 12356 (GH).

PANAMÁ: East of Las Cascadas, C.Z., Maxon 4894 (GH, NY, S, US); Chepigana, Cana-Cuasi-trail, Darien, M.E. & R.A. Terry 1551 (F, US); Orange River, Killip 2631 (S–PA, US).

CUBA. ORIENTE: Baracoa, Lomas de Cuaba, Ekman 3602 (BM, G, GH, NY, S, US); along Río Buey, n. slope of Sierra Maestra, Morton & Acuña 3687 (GH, K, UC, US); near Monte Verde, Wright 976 in part (B, BM, BR, F, G, GOET, IA, L, LE, MO, S–PA, US).

HISPANIOLA. HAÏTI: Near Plaisance, Dept. du Nord, Leonard 9330 (GH, NY, UC, US).

SAN DOMINGO: Las Cidras, Sabaneta, prov. Monte Cristy, Valeur 548 p.p. mai. (C, F, G, GH, K, MO, US); La Cumbre, Cordillera Central, prov. San Domingo, Ekman H 12361 (B, NY, S, US); Cotuy, prov. de la Vega, Abbott 824 (US, HOLOTYPE of *L. Abbottii;* Isotypes in GH, NY); Jato Viejo R., Samaná-penins., Abbott 1404 (GH, NY, US).

Jamaica: Crown Lands near Troy, Maxon 2925 (NY, S, US); ibid., Harris 8731 (BM, NY); Catalina near Chepstow, A. Moore s.n. (NY, US).

Puerto Rico: El Yunque, Big Tree Trail, Blomquist 13156 (UC, US); Rio Piedras near San Juan, Hioram s.n. (L, M, S–PA, US); Sierra de Luquillo, P. Wilson 204 (GH, NY, US); Utuado, Santa Isabel, Sintenis 6154 (B, G, GH, GOET, K, LE, M, S–PA, US); Fajardo, Heller & Heller 994 (F, K, NY, US).

Guadeloupe: Duss 4240 (NY, US), id. s.n. (C, F, GH, MO, US); L'Herminier s.n. (B, BM, F, G, K, L, LE, MO, NY); Husnot 270 (BM).

Dominica: Eggers 900 (C, F, K, US); id. 647 in part (B, BR, GOET, NY, S–PA, W).

Grenada: Sherring 183 (C, US); Broadway s.n. (GH, NY, US).

Colombia. El Valle: Córdoba, Dagua Valley, Pittier 518, 534 (US); ibid., Killip 5104 (GH, NY, PH, US); Buenaventura, Lehmann 98 (K).

Cundinamarca: Buena Vista, Gazaguan Valley, Grant 10415 (US).

Meta: Sierra Macarena, Philipson 2340 (BM); Puerto Lopez, Little & Little 8314 (US).

Antioquia: Peñas Blancas, Woronow & Juzepczuk 4544 (US); Guadalito, Kalbreyer 1387 in part (B, K).

Santander: Puerto Wilches–Puerto Santos, Killip & A. C. Smith 14837 (NY, US); Barranca Bermeja, Haught 1293, 1352 (GH, US).

Vaupés: R. Guayabero, Cuatrecasas 7552 (US).

Bolívar: Boca Antizales, R. Esmeralda, Pennell 4482 (NY).

Boyaca: Puente Nacional, Karsten s.n. in part (LE).

Chocó: Bay of Chocó, Seemann 979 in part (BM, K).

Venezuela. Amazonas: Tamatama, Upper Orinoco, Ll. Williams 15097 (F, G, US); Yavita, id. 13964 (F, G, US); Capihuara, Upper Casiquiare, id. 15529 (G, US), 15546 (US).

Bolívar: Guaiquinima, R. Paragua, Killip 37479 (GH, US); La Prisión, R. Caura, Ll. Williams 11631 (F, US).

Anzoátegui: Montaña de las Palomas, R. Neverí, Steyermark 61456 (F, NY, US), 61457 (F, US).

Trinidad: Aripo Road, Arima, Broadway 5408 (F, MO, UC, US), 5409 (F, MO, US); Sangre Grande, Broadway 6095 (BM, K); ibid., Britton & Hazen 369 (GH, K, NY, US); ibid., Britton 2838 (GH, NY, S–PA, US); Quare Road-Valencia Forests, Broadway 6299 (BM, F, K, MO, S, W); without loc., Fendler 24 (B, BM, F, G, GH, IA, K, LE, M, MO, NY, PH, S, UC, US); id. 110 (B, BM, F, GH, IA, K, LE, M, MO, NY, UC, US).

Tobago: Eggers 5814 (US), Broadway 3883 (BM).

British Guiana: Tumatumari, Potaro R., Gleason 85 (NY, US); ibid., Linder 22 (GH, NY); ibid., Hitchcock 17356 (GH, NY, US); Kamuni Creek, Groete Creek, Essequibo R., Maguire & Fanshawe 22917 (A, K, NY, U, US); Moraballi Creek near Bartica, Essequibo R., Richards 21, 32, 281, 467 (K), 156, 351 (BM, K); Kamwatta, Pomeroon distr., de la Cruz 1172 (GH, MO, NY, PH, US); Mt. Roraima, Schomburgk 9 (BM); without loc., Schomburgk 148 (BM, G), 251 (B, L), 347 in part (B, BM, G, K, L, US).

Suriname: Nassau Mts., Lanjouw & Lindeman 2312 (BM, U); Upper Nickerie R., Tulleken 512 (L, U); plant. Bergendaal, Focke 1081 (K, U); Tafelberg, Maguire 24244 (A, F, K, MO, NY, S–PA, U, UC, US); Para R. region, Wullschlaegel 693 in part, 1717 (BR); without loc., Hostmann 96 in part (B, BM), 108 (BM, FI, K), 1352c (B).

French Guiana: Near R. Saï, Leprieur 6 (GH, LE, US); Acarouany, Sagot 733 (B, BM, K, NY, S–PA), 841 (B, BM, G, GOET, K, LE, S–PA); without loc., Leprieur 22 (B, GH, LE, NY, US), 162 (FI, P, U), 547 (P, UPS).

Brazil. Amazonas: Manáos, Killip & A. C. Smith 30178 (GH, NY, US); Humayta, between Rs. Livramento and Ipixuna, Krukoff 7302 (GH, NY).

Pará: Acará, Thomé Assú, Mexía 6016 in part (BM, MO, UC, US); Villa Aramá, Huber 1824 (G); Tanaii, R. Acará, Spruce 50 (B, BM, K), 385 (M); near Pará, Miles Moss 14 (BM).

Goias: without loc., Glaziou 22639 in part (B, G, NY).

Bahia: Ilheos, Martius 367 (BR, M, NY); ibid., Riedel 3, 12 (LE); Jacobina, Blanchet 2511 (C, FI, G, K, L, M, S–PA); without loc., Blanchet 2252 (BM, G, US).

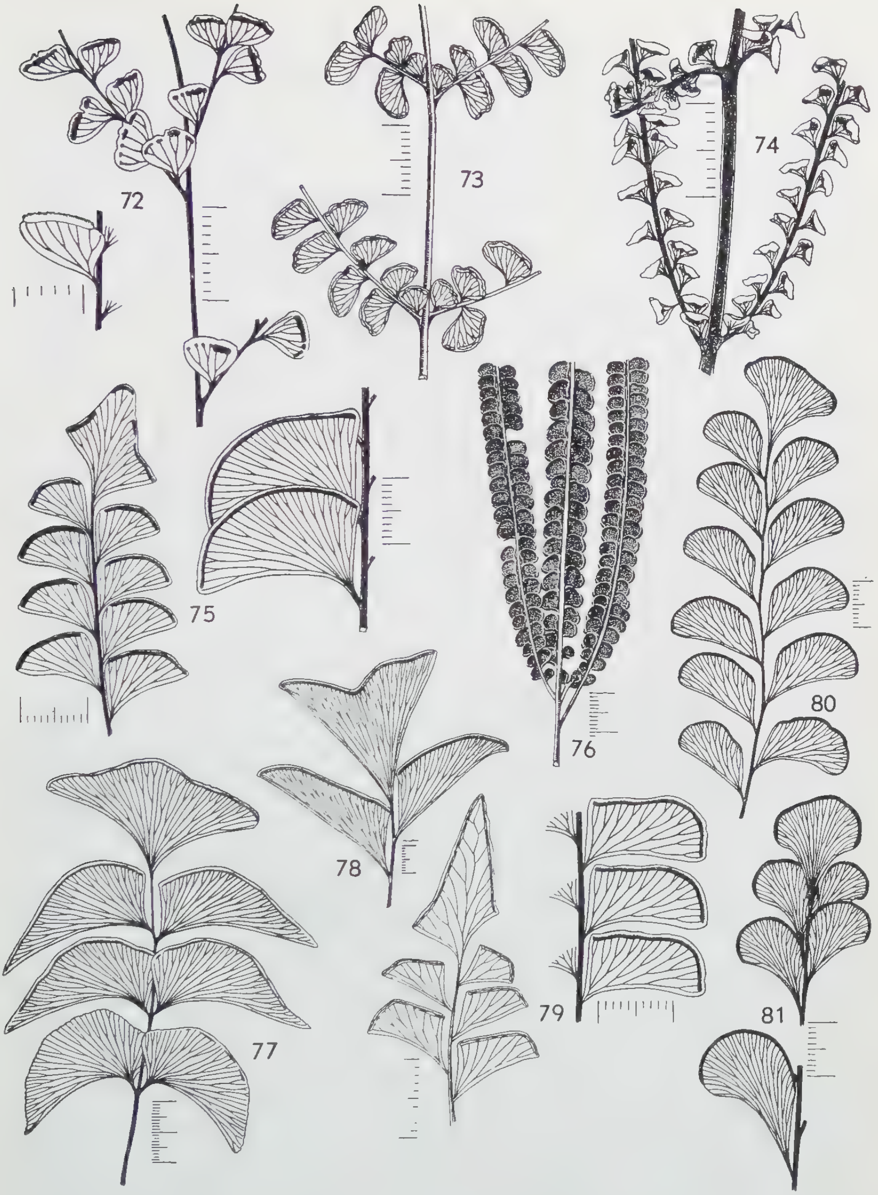


Fig. 72: *Lindsaea filipendula;* middle portion of lamina and pinnule (left) (v. Lützelburg 252). Fig. 73: *L. stricta* var. *stricta* (the lax form); portion from base of lamina (Mosén 74). Fig. 74: *L. stricta* var. *parvula;* portion from base of lamina (Kappler 1737). Fig. 75: *L. lancea* var. *elatior;* apex of lamina (left), pinnules from lower part of lamina (right) (Haught 1364). Fig. 67: *L. stricta* var. *jamesoniiformis;* portion from base of lamina (Maguire 24377). Fig. 77-78: *L. ulei;* fig. 77: complete, largely fertile lamina (Killip 37406); fig. 78: apex of lamina (Ule 5756). Fig. 79: *L. lancea* var. *lancea;* apex (left) and pinnules from base of lateral pinna (right) (Gaudichaud s.n.). Fig. 80: *L. schomburgkii* f. *coriifolia;* upper part of lamina (v. Lützelburg 22956). Fig. 81: *L. schomburgkii* f. *densa;* apex of lamina and pinnule from base (below) (Steyermark 59474). (Scales in mm).

Minas Gerais: Viçosa, Mexía 4639a (GH, UC, US); Lagôa Santa, Warming 61 (C).

Rio de Janeiro: Serra d'Estrella, Beyrich s.n. (L); Rezende, Hoehne & Gehrt 17585 (GH).

São Paulo: Santos, Rio Boturoca, Mosén 3527 (B, BR, S); Sorocaba, Mosén 3056 (S), 3734 (C, L, LE, S, S–PA, UPS); Apiahy, Puiggarí s.n. (GOET).

Matto Grosso: Serra do Itapirapuan, Affonso, Lindman A 3341 (BM, K, S, S–PA); Poaia, Grillos, Lindman A 3253 (S, S–PA); Santa Anna da Chapada, Robert 562 (BM).

Paraná: Jacarehy, Dusén 14643 (C. Chr. in BM, F, NY, PH, S); Paranagua, Herter 20037 (B); Serra do Mar, Volta Grande, Dusén 749a (S, US).

Santa Catarina: Blumenau, Goeden 22 (UC, Holotype of var. *subtripinnata*); ibid., Reitz & Klein 2186 (HBR); ibid., Viereck 76 (M); Joinville, Schmalz 83 (F, MO); Isla Santa Catarina, Gaudichaud 51 (B, FI); Peninsula da Gloria, Ule 30 (B).

Rio Grande do Sul: Porto Alegre, Stier s.n. (Rosenstock-exs. 324) (B, M, S–PA, US); Santa Cruz, Jürgens 315 (NY).

Ecuador: Sapote–Milagro, Crespi s.n. (US); near Quininde, Holdridge 1638 (GH, US); Baños–Pintuo, Stübel 993 (B).

Perú. Loreto: Pongo de Manseriche, Mexía 6207a (GH, UC, US); Iquitos, Killip & A. C. Smith 27021 (NY, US).

Huánuco: Hac. Mercedes, distr. Churubamba, Mexía 8178a (UC).

Junín: Schunke Hacienda above San Ramon, Killip & A. C. Smith 24698 (NY, US); ibid., Schunke A 233 (US); Chanchamayo Valley, Schunke 458 (F, US); Quimiri, Tarma, Esposto s.n. (USM).

San Martín: Near Tingo María, Allard 21369, 21491 (US); ibid., R. M. & A. F. Tryon 5291, 5296, 5297 (U).

Bolivia. La Paz: Mapiri, Rusby 161 (B, BM, G, GH, K, LE, MO, NY, PH, US, W); Choropampa near Mapiri, R. S. Williams 1329 (GH, NY, UC, US); ibid., Buchtien 1101 (B, F, LE, M, S–PA, US); San Carlos near Mapiri, Buchtien 8 in part (MO), 11 (NY, S–PA, UC), 12 (NY, UC), 1002 (NY, US), 1102 (B, S–PA); Copacabana, Larecaja Prov., Krukoff 11264 (F, GH, K, MO, NY, S, U, US).

Paraguay: Yerbales, Sierra de Maracayú, R. Curuguatuy, Hassler 4614 (B, BM, G, GH, NY, S–PA); Paraguari, Cerros de Tobaty, Hassler 6373 (B, BM, G, GH, K, NY, S); Vista Alegre, Rojas 3824, 3851 (C).

Most specimens from Bolivia and Paraguay are atypical, with strongly reduced upper pinnules and a small, not always quite free terminal pinnule; there is perhaps some introgression with *L. quadrangularis* ssp. *terminalis*.

There is no specimen of *Adiantum lancea* L. in the Linnaean herbarium or in the Hortus Cliffortianus. Linnaeus' original description reads as follows:

"Adiantum frondibus pinnatis: pinnis oppositis oblongis: terminalibus triangulari hastatis. +. Adiantum album maximum americanum. Seb. thes. 2. p. 65. t. 64. f. 7, 8. Habitat Surinami.

Stipes laevis. Frons pinnata: foliolis lateralibus oppositis, brevioribus, saepe duorum parium: impari longiore. Pinnae recurvatae, oblongae, obtusae: terminales majores, cordato s. hastato-triangulares, oblongae, acutae."

Seba's plate (1735) shows two almost identical bipinnate leaves which are in exact agreeance with this description. His comment is: "Adiante, ou Capillaire, d'Amerique, blanc, à grandes feuilles. Cette Plante qu'on m'a envoyée de Surinam, pousse des tiges menues, rondes, garnies de feuilles opposées, d'un verd-pâle. Ses vertus sont pectorales, telles que celles du Capillaire de nos climats, dont l'usage si efficace contre la Toux & les autres maladies du Poumon, est connu de tout le monde . . ." It is not entirely certain whether this really applies to *Lindsaea lancea*. The petiole of the bipinnate form of that species is not round, and the base of the terminal pinnule is never cordate or hastate. This may, however, be an exaggeration of the plate. Furthermore, there is no species of *Adiantum* occurring in Suriname known to the writer which the plate might represent; all have even more different terminal pinnules. Therefore it seems reasonably safe to assume that Seba's plant was really *Lindsaea lancea*. Linnaeus' description was presumably drawn from Seba's plate—all characters mentioned by him can be observed there—and it is best to regard this plate as the type of the species.

b. var. **remota** (Kunze) Kramer, comb. nov. **Fig. 29**

Basionym: *L. pumila* Klotzsch var.? *remota* Kunze, Linnaea 21:226 (1848).

Type: Kegel 1066 from Sornau Creek near Joden-Savanne, Suriname (GOET!).

Heterotypic synonym: *L. pusilla* Splitgerber, Tijdschr. Nat. Gesch. Physiol. 7:423 (1840); Kuhn, Chaetopt. 25 (1882); Posthumus, Fl. Surin. Suppl. 75 (1928). Type: Splitgerber 108 from the vic. of Paramaribo, Suriname (L!).

Rhizome slender, ca. 1 mm in diam.; scales as in var. *lancea* but smaller, up to 1 mm long, 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* close, ca. 3–18 cm long, half as long to about as long as the lamina, ½–1 mm in diam. near the apex, reddish-brown to atropurpureous, ± shining, adaxially sharply angular almost to the base, the angles paler above, the surface channelled, abaxially similar above, below mostly subterete. *Lamina* pinnate or bipinnate, dark brownish-green or olivaceous, herbaceous, ca. 5–16 cm long, with up to 2 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, pale above; axillary cushions not seen. *Pinnae* (and, mutatis mutandis, simply pinnate laminae) subopposite, ascending under an angle of ca. 30–45°, 6–12 cm long, 2–3 cm wide, the terminal mostly longest, widest slightly above the base, gradually narrowed to the apex. Secondary rachises similar to the primary but abaxially with a terete portion at the base; rachis of terminal pinna and of simply pinnate laminae abaxially channelled throughout. *Pinnules* 6–15 to a side, alternate or the lower ones subopposite, spreading or slightly ascending, the lower ones often somewhat deflexed, subsessile, rather far apart, not contiguous, 10–16 mm long, 5–8 mm wide, mostly ca. 12 × 6 mm, ca. 2 × as long as wide, semi-elliptic or mostly semi-oval, more strongly narrowed to the apex than in var. *lancea*, mostly subacute. Inner margin straight, divergent or parellel to slightly overlapping the sec. rachis, lower base cuneate, somewhat stalk-like, upper base shortly rounded or angular, lower margin straight of faintly convex, concave in deflexed pinnules, upper margin straight at the base, convex towards the apex, mostly without a separate outer margin, sometimes minutely erose. Marginal thickening stramineous, inconspicuous except at the base of the lower margin. Upper/outer margin of sterile pinnules shallowly crenate, the incisions up to ½ mm deep, the lobes broadly rounded or flattened. Veins immersed, once or twice forked, their ends ca. ¾–1 mm apart. Upper pinnules not strongly reduced, 5–8 mm long. Terminal pinnule triangular-lanceolate, acute or mostly obtuse, cuneate-narrowed at the asymmetrical base, 1–1.5 cm long, soriferous in the lobes at the base or throughout. *Sori* as in var. *lancea*, but the indusium mostly superficially erose, but little reflexed at full maturity. Sporangia ca. 175 × 160 μ; annulus with 10–12 indurated cells; spores trilete, pale yellowish-brown, ca. 23–28 μ.

Distribution: Northern South America; apparently uncommon (map 40). In moist forests at lower elevations; almost always along watercourses.

Colombia. Amazonas/Vaupés: Sorotama, Río Apaporis, above mouth of R. Kananarí, Schultes & Cabrera 16073 (US).
Venezuela. Bolívar: R. Tonoro, above junction with R. Paragua, Killip 37411 (US).
British Guiana: Sheenabowa, Potaro R., Jenman s.n. (NY); Porato R., Jenman s.n. (NY); Kurupung, Leng 268 (NY); Kaieteur Falls, Appun s.n. (B); ibid., Jenman 1392 in part (K); Essequibo R., Persaud 355 in part (F); without loc., Drake s.n. in part (NY).
Suriname: Forest near Paramaribo, Splitgerber 108 (L, Holotype of *L. pusilla*); Sornau Creek near Joden-Savanne, Kegel 1066 (GOET, Holotype); along Wane creek between Moengo tapoe and Grote Zwiebelzwamp, Lanjouw & Lindeman 516 (BM, U); plant. Berlijn (Compass), Para R., Wullschlaegel 693 in part (BR).
Brazil. Pará: Acará, Thomé Assú, Mexía 5948a (C, K); ibid., id. 6016 in part (B, C, F, G, GH, K, NY, PH, S, U, UC).

The combination of dark petioles and small, more strongly narrowed, less close pinnules serves to distinguish this variety. Transitions to var. *lancea* are quite rare; an example is Killip & Cuatrecasas 38883a from Agua Clara, El Valle, Colombia (F), an epiphytic, perhaps depauperate specimen.

c. var. **elatior** (Kunze) Kramer, comb. nov. **Fig. 75**

Basionym: *L. falcata* Dryand. var. *β elatior* Kunze, Linnaea 21:225 (1848).

Type: Kegel 1068 from Sornau Creek near Joden-Savanne, Suriname (Goet!).

Rhizome 1.5–2 mm in diam.; scales up to 1.5 mm long, otherwise as in var. *lancea*. *Petioles* close, 10–37 cm long, half as long to about as long as the lamina, ¾–1¼ mm in diam. near the apex, dark olivaceous to dark reddish brown or castaneous, rather dull, adaxially flattened or sulcate almost to the base, abaxially at least in the upper third sharply angular, the surface between the angles flattened or shallowly sulcate, below gradually obtusely angular or subterete; the angles mostly paler when sharp. *Lamina* simply pinnate, medium or brownish green, herbaceous, linear, 16–ca. 40 cm long, 3–5 cm wide, mostly widest at the base or just above the base, with (20–)25–40 pinnules to a side and a separate terminal one. Primary rachis reddish or castaneous, sharply angled, the angles mostly paler, and ± sulcate. *Pinnules* alternate or the lower ones subopposite, close, sometimes contiguous or slightly overlapping, subsessile, spreading, the basal ones sometimes slightly deflexed, resembling ¼ of an ellipse, not rarely subfalcate, the largest 15–25 mm long, 8–14 mm wide, 1½ to almost 2 × as long as wide. Inner margin approximately straight, lower base cuneate, ± stalk-like, upper base shortly rounded or subangular, upper margin evenly convex or less so towards the base, lower margin ± concave, apex obtuse or subacute; no separate outer margin developed. Marginal thickening present throughout, inconspicuous except at the base of the lower margin; all margins entire, the upper/outer margin of sterile pinnules very shallowly crenate. Veins immersed but often visible as wrinkles in the leaf-tissue, 2–3 times forked, about 1 mm apart at the margin; main vein hardly united with the marginal strand, often reddish at the base. A few lower pinnules sometimes slightly shortened, the upper ones more strongly reduced, 9–10(–12) mm long, about ½ the size of the lower ones. Terminal pinnule asymmetrically-triangular or rhombic, ca. 1–2 cm long, lobed at the base, very obtuse, with an almost percurrent midvein, soriferous in the lobes, sometimes also in the apical part. *Sori* as in var. *lancea*, but the indusium often closer to the margin. Sporangia ca. 165 × 120 μ; annulus with 9–11 indurated cells; spores as in var. *lancea*, ca. 28 μ.

Distribution: Northern and central South America (map 39). In forests, sometimes in bogs, at lower elevations.

COLOMBIA. EL VALLE: Buenaventura, André 275 (K).

SANTANDER: Vic. of Barranca Bermeja, Magdalena Valley, Haught 1364 (GH, UC, US).

VAUPÉS: Cerro Isibukuri, Río Kananarí, Schultes & Cabrera 14446 (US).

BRITISH GUIANA: Essequibo R., Appun 54 (B); Upper Rupununi R., near Dadanawa, de la Cruz 1556 (F, GH, K, MO, NY, PH, UC, US).

SURINAME: Sornau–Creek near Joden-Savanne, Kegel 1068 (GOET, HOLOTYPE); perhaps also Hostmann 108 without loc. (FI, GOET, K; mat. incomplete, doubtful).

BRAZIL. MATTO GROSSO: Campo Teles Pires, Sick B 535 (RB).

There are a few simply pinnate specimens of var. *lancea* that approach var. *elatior* in general habit; they differ in acute or subacute terminal pinnule and less reduced upper pinnules; an example is Riedel 18a from Castelnovo, Brazil (B, C, FI, GOET, LE, M, S-PA). These specimens are not numerous, and var. *elatior* is sufficiently distinct from the very large series of specimens of var. *lancea* now extant to be maintained as a variety.

d. var. **falcata** (Dryand.) Rosenstock, Hedwigia 46:79 (1906), as to type only; incorrectly publ. as new comb. by Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928). **Fig. 30**

Basionym: *L. falcata* Dryander, Trans. Linn. Soc. 3:41 (1797),t. 7 fig. 2; Roem. Arch. 2 (II):236 (1801), t. V fig. 5; Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V: 422 (1810); Sprengel, Syst. Veget. IV:79 (1827); Desvaux, Prodr. 313 (1827); Klotzsch, Linnaea 18:545 (1844); Kunze, Linnaea 21:224 (1848); Bot. Zeit. 8:348 (1850); J. Smith, Hist. Fil. 268 (1875); Jenman, W. Ind. Gui. F. 74 (1899), in part; Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. VII:374 (1918); Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. min.; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930); A. C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931); Alston, Kew Bull. 1932:311; Posthumus, Rec. trav. bot. néerl. 31:469 (1934); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948), in part.

Type: Aublet s.n. from French Guiana (P? not seen).

Homotypic synonyms: *L. trapeziformis* var. *δ falcata* (Dryand.) Baker, Fl. Bras. I/:355 (1870), in part, excl. synon.

L. lancea (L.) Bedd. f. *falcata* (Dryand.) Lindman, Ark. f. Bot. 1:201 (1903).

Rhizome creeping, often widely and much branched, 1–2 mm in diam.; scales up to 1 mm long, otherwise as in var. *lancea*. *Petioles* close, (5–)7–22, mostly about 10–16 cm long, $^2/_3$–1½ × as long as the lamina, 0.5–1 mm in diam. near the apex, reddish-brown to atropurpureous or almost black, shining, adaxially sharply angular almost to the base, above with pale sometimes wing-like angles which evasnesce downwards, abaxially with similar angles above, these rather abruptly evanescing about halfway, the lower half obtusely angular or subterete; the surfaces between the angles slightly convex to concave. *Lamina* simply pinnate, yellowish to olivaceous, herbaceous, broadly ovate to narrowly lanceolate, (5–)10–25, mostly 12–20 cm long, 4–7½ cm wide, relatively widest in short specimens, with 3–15 (rarely more, in atypical specimens) pinnules to a side and a large separate terminal one. *Rachis* similar to the upper part of the petiole, the pale angles more pronounced, sometimes distinctly wing-like, the surfaces sulcate. *Pinnules* alternate or the lower ones subopposite, spreading or, especially the upper ones, somewhat ascending, the lower ones mostly deflexed, the basal pair often strongly, separated by spaces equal to half their width to contiguous or slightly overlapping, subsessile, subtrapeziform to elongate-dimidiate-elliptic, faintly to strongly falcate, at least the basal ones, the largest 21–45 mm long, 11–20 mm wide, 2–3 × as long as wide, mostly widest at base or in the basal $^2/_3$. Inner margin ± straight and parallel to the rachis, lower base cuneate, slightly stalk-like, upper base shortly rounded to subangular, lower margin mostly concave, in the basal pinnules often strongly so, upper margin straight at the base, increasingly convex towards the apex, in the basal pinnules often evenly convex, a separate outer margin sometimes present; apex subacute or almost obtuse, mostly pointing obliquely downwards, the pinnules slightly hamate. Marginal thickening stramineous, present throughout, inconspicuous. All margins entire, upper/outer margin of sterile pinnules subentire to shallowly crenate. Veins immersed except at their extreme bases, mostly 2 or 3 times forked, lax, 1–1.5 mm apart at the margin. Main vein hardly or not united with the marginal strand, ca. $^3/_4$ mm above it almost from the base. Lower pinnules not reduced, but, as they are often deflexed, the lamina slightly narrowed at the base; upper pinnules not at all or slightly reduced (in extreme cases not quite $^2/_3$ the length of the lower ones). Terminal pinnule large, very asymmetrical, approximately triangular, trilobed, one basal lobe of ca. 2 cm, another about half as long, opposite and above the other, the central lobe as large as the basal one or larger, the whole pinnule 3–5 cm long and broad, acute or shortly acuminate, the base below the lobes long-cuneate, a percurrent midvein present. *Sori* continuous along the upper/outer margin, and in the basal lobes of the terminal pinnule, sometimes also in the central lobe. Indusium and sporangia as in var. *lancea*.

Distribution: Panamá and tropical South America; less common than var. *lancea* (map 38). In moist forests, occasionally in swamps, terrestrial or on decaying wood, rarely epiphytic, from sea-level to ca. 1000 m.

Representative specimens:

Panamá: Southern Darien, Seemann s.n. (BM).

Colombia. El Valle: Buenaventura, Killip 11740 (GH, PH, US).

Chocó: La Concepción, east of Quibdó, Archer 1992 (GH, US).

Vaupés: Cerro de Circasia, Cuatrecasas 7175 (F, US), 7184 (F); Sorotama, Río Apaporis, Schultes & Cabrera 15999 (US).

Venezuela. Amazonas: Slopes of Mt. Duida, Tate 904 (NY, US); Tamatama, Upper Orinoco, Ll. Williams 15096 (F, G, US), 15843 (US); Yavita, Ll. Williams 13970 (F, US); Capihuara, Upper Casiquiare, Ll. Williams 15534 (G, US).

Bolívar: Ptari-tepuí, Steyermark 59427 (F, MO, NY, US); Chimantá Massif, slopes of Abácapa-tepuí, Steyermark 74742 (US).

British Guiana: Essequibo R., Appun 67 (B); Macouria Creek, Essequibo R., Jenman s.n. (NY); ibid., Fanshawe M 312 (BM); Bartica-Potaro Road, Sandwith 1141 (BM, K, NY); near mouth of Onoro Creek, Essequibo basin, A. C. Smith 2783 (GH, K, NY).

Suriname: Coppename R. headwaters, Maguire 24181 (A, F, K, MO, NY, U, US); Tafelberg, Maguire 24736 in part (K, NY, U, US); Wilhelmina Mts., Top 1200, Boschwezen 7088 (U); Rikanau near Moengo, Lindeman 6001 (U).

French Guiana: Acarouany, Sagot 734 in part (B, BM, GH, GOET, K, W); Saï R. headwaters, Leprieur 35 (C. Chr. in BM, F, GH, LE, US); Mana, Perrottet s.n. (FI, G); Saï and Conana, Leprieur 160 (FI, P, U); without loc., Jelsky 24 (LE).

Brazil. Amazonas: Humayta, basin of Rio Madeira, Krukoff 7298 (BM, F, GH, K, LE, MO, NY, S, U, US); São Gabriel da Cachoeiras, Rio Negro, Spruce 2356 in part (K, LE); Cucuí, Rio Negro, Baldwin 3206 (US); British Guiana Boundary, Akarai Mts., A. C. Smith 2973 (GH, NY); Venezuelan Boundary, foothills of Serra Imeri near Salto de Huá, Holt & Blake 493 (NY, US).

Pará: Pará, Pételot s.n. (F); ibid., Spruce 47 (K); São Joaquim near Pará, Schwacke 4090 (GOET); Utinga waterworks near Pará, Miles Moss 7 (BM).

Bahia: Blanchet 2226 (B).

Perú. Loreto: Mishuyacu near Iquitos, Klug 379 (F, NY, US), 1510 (F, NY, US); Timbuchi, Upper R. Nanay, Ll. Williams 954 (F); Pongo de Manseriche, Upper Marañon, Tessmann 4850 (B).

Junín: Near La Merced, Killip & A. C. Smith 23966 in part (F, US).

Bolivia. La Paz: San Carlos near Mapiri, Buchtien 8 in part (NY, S–PA, UC, US), 1104 (S–PA, US).

Generally, this variety can be distinguished by its elongate, ± falcate pinnules, the upper ones being hardly reduced, and the very broad, very asymmetrical terminal pinnule. These characters are clearly visible in Dryander's plate of the type specimen, which has not been examined itself by the author. If applied to this form only, not to all simply pinnate specimens otherwise agreeing with *L. lancea* var. *lancea*, *L. falcata* can be maintained as a variety. There are, however, a few intermediates between these two varieties, e.g. Killip & Cuatrecasas 39083 from Chocó, Colombia (F, K, MO, Pic.-Ser., UC), Lehmann 98 from Buenaventura, Colombia (B, BM, LE, US), and Broadway 5377 from Trinidad (F). Their number in comparison with the large series of specimens of both varieties is very small. Their distribution is also shown on map 38.

e. var. **leprieurii** (Hooker) Kramer, comb. nov. **Fig. 31**

Basionym: *L. Leprieurii* Hooker, Spec. Fil. I:208 (1847), t. 62 D; Kunze, Linnaea 21:225 (1848); Bot. Zeit. 8:325 (1850); Kuhn, Chaetopt. 26 (1882); not of Ettingshausen, Farnkr. t. 145 fig. 9 (1865); prob. not of Wawra, Bot. Ergebn. Reise Max. Südbras. 192 (1866). Type: Leprieur s.n. from French Guiana (K!).

Homotypic synonym: *L. falcata* Dryand. var. *leprieurii* (Hooker) Jenman, W. Ind. Gui. F. 74 (1899).

Heterotypic synonym: *L. Pittieri* Underwood & Maxon, Smithson. Misc. Coll. 62:17 (1920). Type: Pittier 533 from Córdoba, Dagua Valley, El Valle, Colombia (US!).

Rhizome delicate, ca. 1 mm in diam.; *petioles* abaxially terete and black throughout or angular and ± winged near the apex. *Lamina* simply pinnate, herbaceous, dark brownish-green, 3–16 cm long, with 1–14 pinnules to a side which are dimidiate-oblong to falcate, 9–30 mm long, 3–10 mm wide, 2–3 × as long as wide, often decurved, especially the lower ones, the upper ones ± reduced; apex rounded, acute, or apiculate, inner margin not rarely overlapping the rachis. Terminal pinnule relatively large, strongly lobed and asymmetrical at the base. For the rest as the simply pinnate form of var. *lancea*.

Distribution: Northern South America; rare (map 41). Often in mountain forests.

Colombia. El Valle: Córdoba, Dagua Valley, Pittier 533 (US, Holotype of *L. Pittieri;* Isotype in GH); Agua Clara, between Buenaventura and Cali, Killip & Cuatrecasas 38908 (US).

Antioquia: Guadalito, Kalbreyer 1387 in part (B).

Suriname: Near plant. Victoria, Kappler 1353 in part (B, GOET, K, L. S–PA, U, W).

French Guiana: Mountains along Upper Oyapok R., Leprieur 159 in part (B, FI, P); without loc., Leprieur s.n., prob. same coll. (K, Holotype).

This variety in the shape of the terminal and lateral pinnules approaches var. *falcata*, in structure of the petiole the simply pinnate form of var. *lancea*; it is not always easily separated from the latter variety. The specimen described as *L. Pittieri* is apparently depauperate.

Many different, often not at all closely related forms have been put in *L. lancea* (or *trapeziformis*) in the course of time, and many good species that had been described before have been made varieties or synonyms of that voracious species. The most extreme case of this encountered by the author is Baker's treatment in Flora Brasiliensis, whose *L. trapeziformis* contains at least ten different species. Several of his errors appear in Christensen's Index Filicum, though some were corrected in subsequent supplements.

In spite of its great variability, *L. lancea* can be easily distinguished in most cases. Simply pinnate forms can be told apart from other species with once-pinnate leaves and a free terminal pinnule by their triangular or lanceolate terminal pinnule with a distinct apex. The same character serves to distinguish bipinnate forms; in addition, these have a very characteristic structure on the abaxial side of the secondary rachises, where a groove starts abruptly just above the base. This character is shared by *L. arcuata* and *L. quadrangularis* ssp. *antillensis*, which have, however, gradually and strongly reduced, finally ± confluent upper pinnules, and by *L. divaricata*, which has much darker, distinctly winged axes and a not entirely free terminal segment; *L. quadrangularis* ssp. *terminalis* may occasionally have a practically free terminal segment, but here also the axes tend to be darker, and the structure of the abaxial side of the secondary rachises is different. There are, however, a few aberrant specimens of *L. lancea* which have more strongly reduced upper pinnules and a small, not quite free terminal segment; they are much like *L. quadrangularis* ssp. *antillensis*, but differ mainly in the shape of the pinnules (see figs. 53 and 79). The author does not share HODGE's view (1954, p. 102) that these two taxa may be combined. It is not easy to decide which species is the closest relative of *L. lancea*. The most likely one is *L. quadrangularis* (especially ssp. *antillensis* and *terminalis*); *L. divaricata* is perhaps also allied. Relatives in the sub-section *Terminales* are *L. schomburgkii* and *L. ulei*.

For a long time an Asiatic species was included in *L. lancea* (e.g. by BACKER & POSTHUMUS, 1939), which was listed as *L. scandens* Hooker by HOLLTUM (1930, 1954); HIERONYMUS (1920) was of the opinion that its correct name was *L. parasitica* Wall. This author pointed out the principal differences between the Asiatic and the American species very clearly, but even without paying attention to them, the trained eye can tell the two species apart quite readily, although they are similar in general sapect. The writer does not believe that they are at all closely allied; *L. scandens* belongs probably to the group of *L. pectinata*, from which species it can sometimes be separated only with difficulty (HOLTTUM, 1954, p. 328). Nevertheless, the resemblance between *L. lancea* and *L. scandens* presents a case of very striking convergent evolution.

HIERONYMUS (l.c.) argued that Beddome, when making the new combination *Lindsaea lancea* for the Asiatic species, misconstrued

Linaeus' species, as his type was from Suriname, and that he was therefore not the correct author of the combination, which should be ascribed to Mettenius (in Urban, Engl. Bot. Jb. 24:91, 1897). This is, however, not in accordance with our present Code of Nomenclature based on the type-method; Beddome's transfer applied in the first place to Linnaeus' type-specimen, no matter what other specimens were included in the same species.

33. **Lindsaea schomburgkii** Klotzsch, Linnaea 18:545 (1844); Kunze, Farrnkr. II:67, t. 128 (1850); Bot. Zeit. 8:349 (1850); Ettingshausen, Farnkr. 211, t. 143 fig. 4, 5 (1865); Hieronymus, Hedwigia 47:209 (1908); Posthumus, Fl. Surin. Suppl. 71 (1928) in part; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930), pl. VI; pl. XII fig. 5.

Type: Schomburgk 278 from British Guiana (B!).

Misapplied names: *L. trapeziformis* auct. non Dryand.; Hooker, Spec. Fil. I:214 (1844), in part.

L. trapeziformis var. *δ falcata* of Baker, Fl. Bras. I^2:355 (1870) in part, pl. 21 fig. 18, 19; not *L. falcata* Dryand.

L. botrychioides auct. non St. Hilaire; Jenman, W. Ind. Gui. F. 75 (1899); Goebel, Flora N.F. 24 fig. p. 371 (1930).

Petioles reddish to dark purplish brown, quadrangular; lamina simply pinnate, firmly herbaceous to coriaceous; pinnules variable in shape, ca. 2⅓–2½ × as long as wide, rarely more, the upper ones but little reduced; veins elevated; terminal pinnule large, free, very obtuse; sori continuous; spores trilete.

Rhizome short-creeping, 2–3 mm in diam.; scales lanceolate, acuminate, up to 1.5 mm long, 0.3 mm wide, with up to 10 rows of cells at the base. *Petioles* close, ca. 10–35, mostly ca. 15–20 cm long, ¾–1½ × as long as the lamina, 0.5–1.5, mostly ca. 1 mm in diam. near the apex, subterete at the base, adaxially above with a shallow groove, the angles towards the apex sharper, paler, and more protruding, but hardly ever wing-like. *Lamina* 5–50, mostly about 20–30 cm long, 3–10, mostly 4–6 cm wide, with 2–32, mostly about 10 pinnules to a side and a distinct terminal one. *Rachis* similar to the upper part of the petiole but often paler, abaxially sulcate above, the margins of the groove fusing to form a keel in the stalk-like base of the terminal pinnule. *Pinnules* very variable in texture, size, and shape, pale yellowish-green to olivaceous or rather dark brown, semi-ovate, semi-elliptic, subtrapeziform, or broadly falcate, the lower ones subopposite, the upper ones alternate, spreading or mostly more or less ascending, the largest 18–35 mm long, 9–15 mm wide, the greatest width in the lower third or in the middle, sometimes in the upper third. Lower base long-cuneate, somewhat stalk-like, upper base mostly rounded, lower margin straight or shallowly convex or concave, upper margin convex, apex rounded or acute; fertile margin entire or very inconspicuously repand-erose, sterile margin shallowly crenate, the incisions shallow, acute, the lobes rounded, uni- or binerval. Marginal strand present throughout, not very conspicuous except at the lower base, stramineous to pale brown or reddish. Veins raised at least for the basal two-thirds, especially adaxially, 2–3 × forked, their ends ½–1 mm apart, often reddish at the base. Main vein hardly continuous with the marginal strand, ca. 0.2 mm above it near the apex. Terminal pinnule flabellate, resembling undivided leaves of *Ginkgo*, 20–35 mm long, 15–45 mm wide, mostly about as wide as long, slightly convex or subtruncate at the apex, there often soriferous, the sides rounded, rarely acute, the lateral margins concave, the base long-cuneate, venation as in *L. ulei*. *Sori* along the upper/outer margin; indusium rather firm, 0.2 mm wide, entire or minutely erose-sinuate, not quite reaching the margin, ± reflexed at full maturity. Sporangia ca. 195–200 × 140–150 μ; annulus with 11–13 indurated cells; spores pale brownish-yellow, ca. 27–33 μ.

Distribution: Northern and central South America (map 42). Rather euryoeceous; often in exposed situations, on withered rocks, in savannas, in swamps, or in scrub, sometimes also in forests, up to ca. 1600 m.

a. forma **schomburgkii**.

Pinnules acute, strongly ascending, close, overlying the rachis and often also one another, usually firmly herbaceous, venation rather lax.

British Guiana: Swamp behind Oreala, Corantyne R., Im Thurn s.n. (K); ibid., Jenman 435 (K); Essequibo R., Appun 2 (B, W); without loc., Schomburgk 27 (BM, FI, G, W), 278 (B, Holotype), s.n. (L); Appun s.n. (K), 730 (K); Lobscheid s.n. (W).

Perú. San Martin: Pacasmayo–Moyobamba, Pajonal, between Rio Negro and Rioja, Stübel 1059 (B).

b. forma **coriifolia** (Lindman) Kramer, comb. nov. **Fig. 80**

Basionym: *Lindsaea coriifolia* Lindman, Ark. f. Bot. 1:201 (1903), pl. 8 fig. 1; Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Type: unknown coll., "Caracas", Venezuela (S-PA!).

Pinnules acute or obtuse, ascending or spreading, not overlying the rachis, at most touching it, separated by spaces equalling their width or half as wide, or the upper ones contiguous, firmly herbaceous to coriaceous, venation rather close.

Colombia. Amazonas–Vaupés: Río Apaporis, Cachivera de Jirijirimo, Schultes & Cabrera 12459 (US).

Venezuela. Bolívar: Cerro Tonoro, Upper R. Paragua, Cardona 852 (US).

Amazonas: Maroa, R. Guainía, Ll. Williams 14330 (F, US); id. 14264 in part (F); between Esmeralda Savanna and base of Mt. Duida, Steyermark 57819 (F, NY, US); without loc., van Lansberge s.n. (B, L); unknown coll., "Caracas", prob. from southern Venezuela (S–PA, Holotype).

British Guiana: Essequibo, right bank, Guppy 156 (BM); Kaieteur Savannas, Maguire & Fanshawe 23394 (NY, US); Mt. Roraima, Schomburgk 23 (BM); without loc., Jenman (?) s.n. (US).

Brazil. Amazonas: Rio Negro, Içana, Serra de Tunuý, Fróes 22422 (U); Manáos and Flores, Ule 5418 (B, G, K, L); ibid., Miss Solomon s.n. (BM); Içana, Tunuy, von Lützelburg 22956 (M); ibid., Piranana, id. 22988 (M); Rio Uaupés, Panuré, Spruce 2648 (G, GH, GOET); Rio Uaupés, Iutica, Varadouro, von Lützelburg 22762 (M), von Lützelburg 23631 (M); Cachoeira da Turumá, Traill 1355 (K); Flores, von Lützelburg 21980 (M, NY, UC, US); Barra do Rio Negro, Spruce 1371 (K); ibid., id., s.n. (W); São Gabriel da Cachoeiras, Rio Negro, Spruce 2356 in part (LE).

Matto Grosso: Juruana, Hoehne 1817/1818 (NY; unusually large).

Perú. Dept.?: Chamicuras, Bartlett s.n. (W).

c. forma **densa** Kramer, f. nov. **Fig. 71**

Exstat pinnulis approximatis, plus minusve contiguis, valde coriaceis, multum adscendentibus, margine superiore valde convexa, apice obtuso vel rotundato.

Typus: Steyermark 59474 from Ptari-tepuí, Bolívar, Venezuela (F).

Colour pale yellowish-green; marginal strand reddish-brown; veins close.

Only known from Type-collection:
VENEZUELA. BOLÍVAR: Ptari-tepuí, vic. of Misa Kathy camp, low scrubby growth on flat portion of south-facing shoulder, Steyermark 59474 (F, HOLOTYPE; Isotypes in MO, NY, US).

The differences between *L. schomburgkii* and *L. coriifolia*, which were pointed out by Lindman as he described the latter species, break down when more ample material is studied. The form with rather thin, lax, acute, close pinnules to which the type belongs is however rather different in aspect and can be more or less sharply distinguished from the commonest form, f. *coriifolia*, which in itself is quite variable. F. *densa* also is rather outstanding, but as the characters used to separate these forms are all of rather little importance, they are maintained here as *formae* only. It is feasible that eventually they will prove to be quite untenable. In spite of this variability, *L. schomburgkii* can easily be recognized by its simply pinnate lamina with a large, very obtuse terminal pinnule and elevated veins. It is probably closest to *L. semilunata*, which differs mainly by more elongate pinnules.

A series of specimens from the basin of the Kuyuwini R., British Guiana, A. C. Smith 2622 (F, G, GH, MO, NY, S-PA, U, US) is aberrant by very long simply pinnate or rarely subbipinnate leaves, the terminal pinnule approximately rhombic, with an obtuse apex; the spores are abortive. Probably a hybrid, perhaps *L. schomburgkii* × *lancea*. A rather similar specimen, Jenman s.n. (NY) from the Hooroobia Creek, British Guiana, may be of similar origin.

34. **Lindsaea semilunata** (C. Christensen) C. Christensen, Index Filicum 397 (1906). **Fig. 82**

Basionym: *L. lancea* (L.) Bedd. [err.: (L.) Mett.] var. *semilunata* C. Chr., Bot. Tidsskr. 25:81 (1902).

Type: Glaziou 12352, "Brazil", which is Appun (prob. 962) from British Guiana (C. Chr. in BM!).

Misapplied name: *L. trapeziformis* var. δ *falcata* of Baker, Fl. Bras. I²:355 (1870), in part, excl. syn.; non *L. falcata* Dryand.

Petioles castaneous, terete below, quadrangular above; lamina simply pinnate, herbaceous to chartaceous; pinnules elongate-triangular to lanceolate-subfalcate, 3–3½ (–over 4) × as long as wide, the upper ones little or not reduced; veins elevated; terminal pinnule large, free, truncate or concave on the distal side; sori continuous; indusium narrow, entire; spores trilete.

Rhizome creeping, ca. 2 mm in diam.; scales lanceolate, acuminate, up to 0.9 mm long and 0.3 mm wide, with up to about 10 rows of cells at the base. *Petioles* close, rather shining, above with stramineous angles, the surfaces slightly convex, flattened towards the apex, 10–40 cm long, as long as to 1½ × as long as the lamina, 0.5–1 mm in diam. at the apex. *Lamina* 10–25 cm long, 5–10 cm wide, with 4–11 pinnules to a side, the overall number mostly odd, and a large terminal pinnule. *Rachis* similar to the petiole, the angles broader but not wing-like, the surfaces concave. *Pinnules* opposite to alternate, dull olivaceous, 30–45(–70) mm long, 10–14 mm wide, 1–3 cm apart, subsessile, with a long-cuneate, somewhat stalk-like base, broadest just above the base. Inner margin straight or slightly concave, upper margin straight or concave towards the apex, slightly crenate in sterile pinnules, sometimes superficially sinuate or notched in fertile ones, upper base angular or subauriculate, lower edge straight or convex towards the apex; apex subacute to acute, often falcately upcurved, rarely faintly deflexed. Marginal strand stramineous, inconspicuous. Veins, especially abaxially, elevated to about ½ cm from the margin, two to three times forked, ca. 1 mm apart at the margin; main vein not very close to the lower margin, ca. 0.2–0.3 mm above it. Terminal pinnule 2–5 cm long, 3–6 cm wide, triangular to crescent-shaped, as long as wide or wider, the base long-cuneate, passing into a stalk of 0.5–1 cm, the lateral edges concave, the distal edge strongly concave, V-shaped, or straight, soriferous, the sides mostly prolonged into long acute to subacute horns that point to the sides or obliquely upwards; no median main vein present, but two stronger unequal short basal marginal veins can be observed; the keel formed by the fusion of the sides of the channel on the abaxial side of the rachis evanescing in the stalk of the terminal pinnule or running into one of the stronger basal veins. *Sori* along the upper margin, indusium ca. 0.15 mm wide, almost equalling the margin, ± reflexed at full maturity. Sporangia ca. 185 × 140 μ; annulus with 11–12 indurated cells; spores very pale brown, ca. 28–32 μ.

Distribution: Northern South America; apparently rare (map 43). In savannas and forests; very few data extant.

Venezuela. Bolívar: Río Tonoro, Upper R. Paragua, Cardona 829 (NY, US). Amazonas: Yavita, Ll. Williams 13944 (F; slightly aberrant, prob. juvenile).
British Guiana: Cucuyu Creek, Appun 962 (K); Glaziou 12352, "Brazil", almost certainly a duplicate of the preceding number (C. Chr. in BM, Holotype; Isotypes in B, C); id. 12353 (B, C, K; Paratypes).
Brazil. Amazonas: São Gabriel de Cachoeiras, Rio Negro, Spruce 2338 (B, BR, K, W).

To be recognized by simply pinnate leaves with large triangular or crescent-shaped terminal pinnule and elevated veins. It is not closely allied to *L. lancea* var. *falcata* (*L. falcata*), with which Christensen compared it. Closer relatives are *L. ulei*, which has immersed veins and an abaxially largely terete petiole, *L. schomburgkii*, which has more numerous, shorter pinnules and a smaller terminal pinnule, and probably also *L. hemiglossa*, which also has immersed veins and a petiole that is quadrangular almost throughout.

35. **Lindsaea latifrons** Kramer, spec. nov. **Fig. 73**

Folia pinnata, raro bipinnata, petiolo stramineo vel pallide fusco quadrangulari; lamina statu sicco pullo-olivacea, firme herbacea; pinnulis dimidiato-lanceolatis, longitudine latitudinem vulgo ter vel quater superante, apice acuto vel caudato-acuminato, saepe curvato-adscendente, superioribus vix redactis, segmento terminali magno, libero, triangulari vel fere semilunato; soris continuis, indusio angustissimo, integro, marginem paene aequante; sporis tetraedriformibus. Typus: Klug 2890 from Balsapuerto, dept. Loreto, Perú (US).

Rhizome short-creeping, 2–3 mm in diam.; scales as in the following species. *Petioles* closely subdistichous, 15–45 cm long, slightly longer than to 1½ × as long as the lamina, ca. 1½ mm in diam. near the apex, quadrangular, the surfaces channelled or the lateral ones flat, ± shining. *Lamina* ca. 15–38 cm long, 9–16 cm wide (wider when bipinnate), when bipinnate with one patent lateral pinna to a side which is up to 15 cm long, with ca. 6 pinnules to a side, otherwise as simply pinnate laminae, which have 5–14 pinnules to a side and a separate terminal one, equally wide in the lower half, little narrowed towards the apex. *Primary rachis* similar to the petiole, the bottom of the abaxial groove sometimes darker than the rest. Secondary rachises, if any, similar, apart from the terete base of the abaxial side. *Pinnules* subopposite to alternate, subsessile, spreading, or, especially the upper ones, somewhat ascending, the lower ones separated by spaces about equal to their width, the upper ones gradually closer but not contiguous, the lowermost somewhat decurved, 6–9 cm long, 1½–2½ cm wide, broadest at their base or in the lower third. Inner margin ± straight, lower margin often somewhat concave, especially near the base, often concave towards the upcurved apex, upper margin convex, or straight to concave towards the apex, which is acute, rarely obtuse, usually caudate-acuminate and often upcurved; upper base rounded or ± angular, lower base cunate, hardly stalk-like. Marginal thickening not very conspicuous except at the base of the lower margin; all edges entire. Veins immersed, only at the extreme base slightly raised, 2–3 times forked, lax, ca. 1.5–2 mm apart at the margin. Main vein close to the margin but everywhere distinct from it, ca. 0.1–0.2 mm above it. Terminal pinnule variable in size and shape, 2–6 cm long, 3.5–8 cm wide, mostly wider than long, usually asymmetric, the base long-cuneate, with a stalk of ½–1½ cm, the sides straight or concave, the apical margin straight, concave, or sinuous, its apices usually acute or acuminate, sometimes protracted into long upcurved horns; venation about as in *L. ulei*. *Sori* along the upper margin and along the apical margin of the terminal pinnule; indusium 0.1–0.2 mm wide, almost reaching the margin, reflexed at full maturity. No completely sterile pinnules seen. Sporangia ca. 120–130 × 90–100 μ; annulus with 10–12 indurated cells; spores very pale yellowish-brown, ca. 20–23 μ.

Distribution: North-eastern Perú (map 45). In forests, at lower elevations.

PERÚ. LORETO: Balsapuerto, basin of Lower Río Huallaga, Klug 2890 (US, HOLOTYPE; Isotypes in B, BM, F, G, GH, K, MO, NY, S); ibid., Killip & A. C. Smith 28614 (NY, US); ibid., id. 28596 (US); ibid., id. 28614 (NY, US); Tierra Doble, Río Nanay, Ll. Williams 1068 (F).
Dept.?: Chamicuras, Bartlett s.n. (W; immature, somewhat dubious).

Closely related to *L. hemiglossa*, which is distinguished by more slender, elongate pinnules and mostly bright-green colour; perhaps they will eventually prove to be conspecific. The resemblance to *L. ulei* may be due to coindence and not to close alliance; the same is perhaps true for *L. semilunata*. It is possible that the inclusion of *L. hemiglossa* and *L. latifrons* in the present subsection is artificial; they may be more closely related to *L. arcuata* than to *L. lancea* and its allies.

36. **Lindsaea hemiglossa** Kramer, spec. nov. **Fig. 84**

Folia simpliciter pinnata, petiolo rachideque stramineis vel pallide fuscis quadrangularibus, lamina firme herbacea, statu sicco vulgo laetevirens; pinnulis dimidiato-lanceolatis, subacutis, acutis vel longe acuminatis, apice saepe incurvato, longitudine latitudinem quater usque ad sexies superante, pinnulis superioribus vix redactis, segmento terminali magno, libero, fere triangulari vel semilunato; soris continuis; indusio angustissimo, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Schunke A 324 from the Schunke Hacienda above San Ramón, dept. Junín, Perú (UC).

Rhizome creeping, 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1½ mm long and 0.25 mm wide, with up to 8 rows of cells at the base. *Petioles* rather close to close, ca. 10–40, mostly 25–30 cm long, roughly as long as the lamina, rarely much shorter, 1–1½ mm in diam. near the apex, quadrangular except at the extreme base, with channelled surfaces, ± shining. *Lamina* ca. 20–40 cm long, 5–17, mostly 7–9 cm wide, with 7–25, mostly 17–20 pinnules to a side and a separate terminal one, widest at the base or just above it, but little narrowed to the apex. *Rachis* similar to the upper part of the petiole. *Pinnules* subopposite to alternate, subsessile, spreading or mostly more or less ascending, up to 45° in the upper part of the lamina, the lower ones separated by spaces equalling their width or larger, the upper ones closer but not contiguous, often falcately upcurved, 3½–6(–9½) cm long, 0.9–1.5(–1.9) cm wide, broadest at the more or less truncate base. Inner margin straight, lower margin concave at the base, for the rest straight or more often somewhat convex, upper margin convex at the base, thence straight or concave, rarely evenly convex throughout; apex acute (the extreme top often obtuse) to long-acuminate; upper base rounded or ± angular, lower base cuneate, slightly stalk-like. Marginal thickening not conspicuous, stramineous; all edges entire. Veins hidden except at their bases, 2–3 times forked, not close, ca. 1 mm apart at their ends. Main vein close to the margin but everywhere distinct from it, ca. 0.2 mm above it. Terminal pinnule variable in size and shape, 1–6 cm long, 1.5–8.5 cm wide, mostly roughly as long as wide, the base long-cuneate, subsessile or with a stalk of ca. 0.5 mm, the sides straight, concave or S-shaped, the upper margin straight, concave, V-shaped or sinuous, the apices subacute or often protracted into horns that point sideways or upwards; venation mostly as in *L. ulei*. *Sori* along the upper margin and along the apical margin of the terminal pinnule, sometimes leaving the apex free; indusium ca. 0.1 mm wide, not reaching the margin by about its own width, reflexed at full maturity. Sporangia ca. 120 × 95 μ; annulus with 10–12 indurated cells; spores hyaline, almost colourless, ca. 25 μ.

Distribution: Ecuador and Perú (map 45). In dense forests at higher elevations, ca. 1100–1700 m.

ECUADOR. Cuenca, east of the Andes, Pearce 319 (K, W).
PERÚ. JUNÍN: Schunke Hacienda above San Ramón, Schunke A 234 (UC, HOLOTYPE; Isotypes in GH, US); ibid., Killip & A. C. Smith 24571 (F, NY, US); ibid., La Merced, Macbride 5624 (F, US); Chanchamayo Valley, Schunke 511 (F); ibid., id. 806 (F, US); ibid., id. 102 (F, US); Cumbassummun (?) Mts., collector illegib. (K).
SAN MARTÍN: Tarapoto, Spruce s.n. (K).

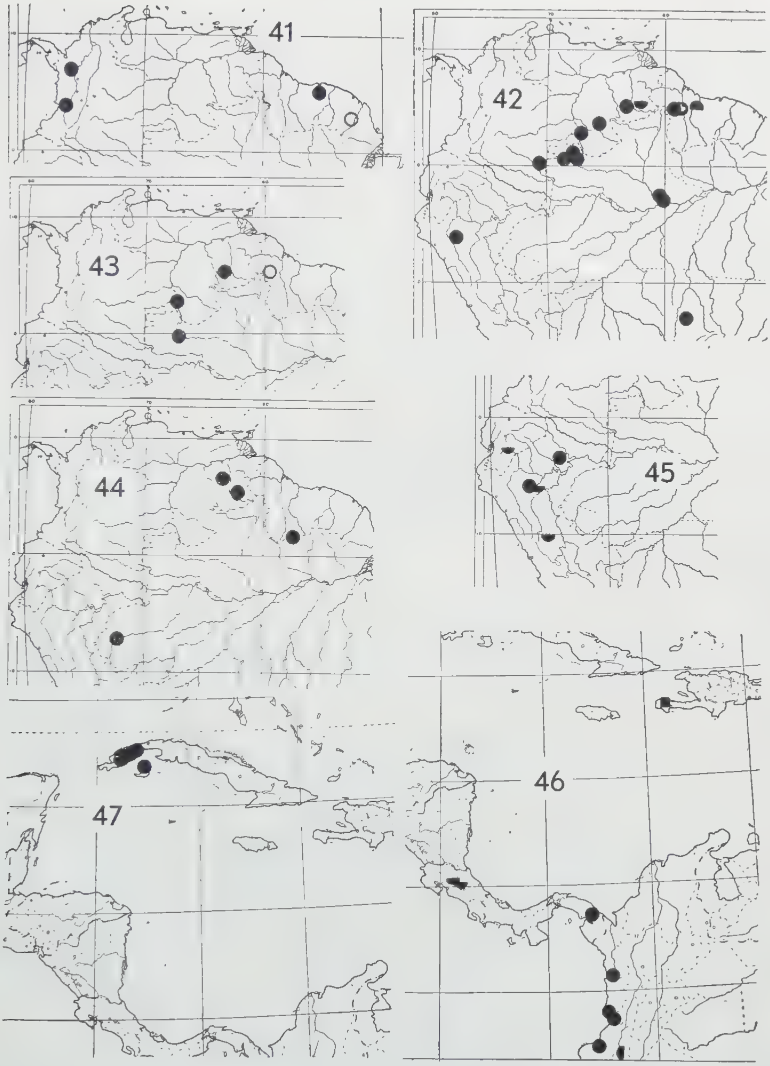
This species is very closely allied to the preceding, where the differences are discussed.

37. **Lindsaea ulei** Hieronymus in Christ, Hedwigia 44:365 (1905); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930). **Fig. 77, 78**

Type: Ule 5756 from Puritisal, Juruá Miry, Rio Juruá, Amazonas, Brazil (B!).

Petioles dark, abaxially terete below, above with pale membranous wings; lamina simply pinnate, herbaceous; pinnules subfalcate-triangular to falcate, 2-2½ × as long as wide, the upper ones little or not reduced; terminal pinnule large, free, asymmetrically flabellate, the distal margin evenly and faintly convex or sinuous; sori continuous; indusium narrow, entire or subentire; spores trilete.

Rhizome creeping, 1–2 mm in diam.; scales narrowly lanceolate, acuminate, up to 1 mm long, 0.2 mm wide, with up to 6 or 7 rows of cells at the base. *Petioles* not very close, 8–30 cm long, 1½–2 × as long as the lamina, ½–1 mm in diam. near the apex, rather lustrous, adaxially flattened, the margins in the upper part pale, membranous, wing-like. *Lamina* dark, dull greenish-brown, ca. 6–20 cm long, 5–13 cm wide, with 1–7 pinnules to a side and a large terminal one. *Rachis* similar to the apical part of the petiole, often paler, more reddish. *Pinnules* subopposite or alternate, subsessile, spreading or the lower ones somewhat deflexed, not contiguous, 2–3 cm apart, 4–7 cm long, 1½–2½ cm wide, acute or shortly acuminate, rarely obtuse, often with a small ± upturned apiculus. Inner margin straight or slightly concave, slightly divergent to slightly overlying the rachis, lower base cuneate, somewhat stalk-like, upper base angular or shortly rounded, lower margin straight or, especially near the base, concave, sometimes slightly



Map 41: *L. lancea* var. *leprieurii*. Map. 42: *L. schomburgkii;* complete dots: f. *coriifolia;* half dots (upper half): f. *schomburgkii;* half dots (lower half): f. *densa*. Map 43: *L. semilunata*. Map 44: *L. ulei*. Map 45: complete dots: *L. latifrons;* half dots: *L. hemiglossa*. Map 46: complete dots: *L. seemannii* var. *seemannii;* half dot (left half): var. *serrigera;* half dots (lower half): *L. pratensis;* square: *L. protensa*. Map 47: *L. cubensis*.

convex near the apex, upper margin convex, mostly less so towards the apex and at the base. Marginal thickening stramineous to pale brown, rather inconspicuous. Upper/outer margin entire in fertile pinnules, shallowly crenate in sterile ones. Veins immersed, mostly twice, rarely three or four times forked, their ends 1–1½ mm apart. Terminal pinnule very large, as large as or larger than the lateral ones, with a stalk of ½–2 cm, 3–5 cm long, 5–11 cm wide, 1½ to more than 2 × as wide as long, the sides straight or somewhat concave. the distal margin entire when soriferous, crenulate when sterile, the sides acute or rounded. No main vein present; for details of the venation see p. 129. *Sori* along the upper/outer margin; indusium ca. 0.2 mm wide, not reaching the margin by about twice its width, reflexed and conceiled at full maturity. Sporangia ca. 135 × 90 μ; annulus with 9–11 indurated cells; spores very pale brownish-yellow, ca. 20–23 μ.

Distribution: Northern South America; apparently rare (map 44). Terrestrial or on tree-trunks, in moist forests, ca. 300–800 m.

VENEZUELA. BOLÍVAR: Río Tonoro, above junction with R. Paragua, Killip 37406 (GH, US); Chimantá Massif, Abácapa-tepuí, Steyermark 74756 (F).
BRAZIL. AMAZONAS: Rio Juruá, Puritisal, Juruá Miry, Ule 5756 (B, HOLOTYPE; Isotypes in G, K, L).
PARÁ: Acarai Mts., Boundary of British Guiana, between drainage of Rio Mapuera and Shodikar Creek, A. C. Smith 2973a (GH, NY).

This species is probably related to *L. lancea* on the one hand and to the section *Haplolindsaea* on the other.

Sectio V. **Haplolindsaea** Kramer, sect. nov.

Lamina simplex, cordato-rotundata, reniformis vel sagittata, petiolo atrato abaxialiter tereti vel superne angulari, soris continuis vel apice laminae interruptis, indusio angusto, valde intramarginali.

Species typica: *Adiantum sagittatum* Aublet (=*Lindsaea sagittata* (Aubl.) Dryand.).

38. **Lindsaea sagittata** (Aublet) Dryander, Trans. Linn. Soc. 3:40 (1797); Roem. Arch. 2 (II):235 (1801); Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V:420 (1810); Sprengel, Syst. Veget. IV:79 (1827); Hooker & Greville, Icon. Fil. I t. 87 (prob. 1828); Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:203 (1844); Fée, 11me mém. 17 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 109; Baker, Fl. Bras. I2:357 (1870), pl. 41 fig. 6; J. Smith, Hist. Fil. 267 (1875); Kuhn, Chaetopt. 25 (1882); Krug in Urban, Engl. Bot. Jb. 24:92 (1897); Christ, Farnkr. d. E. 295 (1897), with fig.; Jenman, W. Ind. Gui. F. 72 (1899); Goebel, Organogr. d. Pfl. II fig. 1126 (1918); Posthumus, Rec. trav. bot. néerl. 23:397 (1927), in part; Fl. Surin. Suppl. 69 (1928), in part; Rec. trav. bot. néerl. 31:469 (1934), in part. **Fig. 88**

Basionym: *Adiantum sagittatum* Aublet, Hist. Pl. Gui. II:964, IV, pl. 366, 1 (1775); J. Smith, Mém. Acad. Roy. Sci. Turin 413 (1793); Poiret in Lamarck, Encycl. Suppl. I:139 (1810).

Type: Aublet s.n., from French Guiana (prob. P, not seen; Isotype in BM!).

Homotypic synonym: *Schizoloma sagittatum* (Aublet) Diels, N. Pfl. I4:218 (1902); Bonaparte, Notes Ptérid. IV:87 (1917); ibid. VII:374 (1918); Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930).

Petioles dark, abaxially terete; lamina simple, sagittate, hastate, or acuminate-cordate, herbaceous; sori continuous or mostly interrupted in the acumen; indusium entire or slightly sinuous, strongly intramarginal; spores trilete.

Rhizome short-creeping, slender, ca. 1–1.3 mm in diam.; scales lanceolate to almost linear, long-acuminate, up to 0.8 mm long but mostly much shorter, usually 0.4–0.6 mm, up to 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* rather close, 4–21 cm long, mostly longer than the lamina, up to three times its length, in small leaves of equal length or shorter, $^3/_4$–1 mm in diam. below the base of the lamina, the extreme apex sometimes broadened; shining, abaxially terete up to the base of the lamina, where the sclerotic tissue is divided, the lateral parts evanescing in the basal portion of the edge of the lamina, the middle portion depressed, V-shaped, prolonged into a tapering point which extends some distance along the midrib; adaxially terete at the base, the upper half or two-thirds with concolorous or paler lateral ridges, these more pronounced towards the apex where the portion between them is flattened or concave. Apparently the petiole is of delicate structure as it is often crushed in dried specimens. *Lamina* dark brownish green, 4–12 cm long, 3.5–10 cm wide, mostly somewhat longer than wide, short- to mostly long-acuminate, the acumen 1–6 cm long, its apex acute or subacute. Sides of the lamina rather evenly convex except towards the apex where they are straight to concave; the same holds for the basal lobes when they are acute. Base deeply cordate, the sinus 1.5–3 cm deep, mostly shortly rounded at the point of attachment of the petiole. The lateral lobes show all transitions from broadly rounded via angular to acuminate, the acumen up to 2 cm long, obtuse to subacute, mostly pointing to the sides; rounded basal lobes sometimes overlapping. Acute or acuminate lobes are generally more common than obtuse ones. Leaves with one acute and one obtuse lobe are extremely rare. Edge entire or very slightly sinuous or crenulate, especially in sterile leaves or portions of leaves, not thickened, except at the base of the sinus. Veins 2–3(–4) times dichotomously forked, a median, flexuose midrib present which extends into the apex and gives off 5–9 lateral veins at each side, apparently not homologous to the submarginal main vein of dimidiate pinnules. Veins immersed, lax, their ends 1–1.5 mm apart, free, but in large leaves often a few anastomoses present. *Sori* leaving the sinus free or reaching about halfway down; indusium thin, greyish or brownish, 0.2–0.4 mm wide, not reaching the margin by 1.5–2.5 mm, bulging or reflexed at maturity. Sporangia ca. 150 × 100–110 μ, annulus with 10–12 indurated cells; spores pale yellowish, ca. 20–25 μ.

Distribution: Guianas (map 48). Terrestrial in forests, from ca. 500–1000 m; very few ecological data extant. Not often collected, but according to Jenman common in the interior of British Guiana.

British Guiana: Kaieteur Falls, Appun s.n. (BM); Pacatout, below the Kaieteur, Jenman 1393 (K); Essequibo R., Appun 42 (B, W); Tiger's Leap, Demerara R., Jenman s.n. (NY); Mazaruni R. below Kalacoon, Jenman s.n. (NY); Amacuro, Goebel s.n. (B, M, P); without loc., Mrs. Gordon s.n. (BM); Appun s.n. (K); Jenman 930 (US); Winter s.n. (UC).
Suriname: Wilhelmina Mts., Top 1200, Stahel 7087 (U); Hendriktop, Boschwezen 5724 (Pic.-Ser., U); Brownsberg, Boschwezen 587 (P, U, US).
French Guiana: without loc., Aublet s.n. (BM, Isotype); Poiteau s.n. (K).

Erroneously reported from Guadeloupe by Sprengel, l.c., and by some other authors, apparently on his authority. Said to occur in Venezuela by Knuth, l.c., and in Trinidad by Krug, l.c.; no specimens seen by the writer.

L. sagittata is not likely to be confused with any other species; the simple acuminate lamina is quite unique. Posthumus (1927) united it with *L. reniformis;* for arguments against this, see under the latter species.

39. **Lindsaea reniformis** Dryander, Trans. Linn. Soc. 3:40 (1797), t. 7 fig. 1; Roem. Arch. 2 (II):235 (1801), t. IV f. 1; Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V:420 (1810); Sprengel, Syst. Veget. IV:79 (1827); Desvaux, Prod. 312 (1827); Kunze,

Farrnkr. I:31 (1840); t. 16 fig. 2; J. Smith, Lond. Jo. Bot. 1:200 (1842); Klotzsch, Linnaea 18:544 (1844); Hooker, Spec. Fil. I:203 (1844); Ettingshausen, Farnkr. 211 (1865), t. 145 fig. 10; Hooker & Baker, Syn. Fil. 1st. ed. (1868), 2nd ed. (1874) 109; Baker, Fl. Bras. I^2:357 (1870), in part; J. Smith, Hist. Fil. 267 (1875); Christ, Farnkr. d. E. 294 (1897); Jenman, W. Ind. Gui. F. 72 (1899); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Type: Alex. Anderson s.n. from Suriname (BM!).

Homotypic synonyms: *Schizoloma reniforme* (Dryand.) Diels, N. Pfl. I^4:218 (1902); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930). *Adiantum emarginatum* Poiret in Lamarck, Encycl. Suppl. I:139 (1810), non Bory, 1810, nec Hooker, 1851.

Misapplied name: *L. sagittata* auct. non Dryand.; Posthumus, Rec. trav. bot. néerl. 23:397 (1927), in part; Fl. Surin. Suppl. 69 (1928), in part; Rec. trav. bot. néerl. 31:469 (1934), in part; Wagner, Am. Jo. Bot. 39 fig. 9 I (1952).

Petioles dark, abaxially terete or with short, irregular, interrupted lateral ridges below the apex; lamina simple, bean-shaped, reniform or suborbicular, herbaceous to subcoriaceous; sori continuous; indusium subentire, strongly intramarginal; spores trilete.

Rhizome short-creeping, 1½–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long and 0.2 mm wide, with up to 5 rows of cells at the base, the greater part of 1 or 2 rows of cells only. *Petioles* rather close to close, subdistichous, 6–ca. 30 cm long, 2–3 times as long as the lamina, 0.6–1 mm in diam. at the base of the lamina, very shining, abaxially terete or with short, irregular, interrupted lateral ridges below the apex which are not or hardly discoloured, adaxially terete in the lower half, in the upper half flattened, with lateral ridges which are pale and wing-like towards the apex where they are continuous with the margin of the blade. *Lamina* (1.5–)3–10 cm long, (3–)4.5–10 cm wide, mostly about 1 cm wider than long, sometimes as long as wide, or, in small bean-shaped leaves up to twice as wide as long, greatest width lying at the middle or at the level of the insertion of the petiole, medium to dark or brownish green on the ventral, paler on the dorsal surface; margin more or less equally rounded, but often with a more protruding portion at the distal side, the sinus rather narrow, about 1.5–3(–4) cm deep extending to about ⅓ of the length of the lamina, in small leaves sometimes almost absent, the base shallowly concave; rarely the basal lobes, which are always broadly rounded, overlap in very large leaves. The sclerotic patch at the base of the lamina adaxially as in *L. sagittata*, abaxially with two lateral more or less truncate portions and a middle shank which is linear, tapering, and extends up to 8 mm into the blade. Veins all dichotomous *), two to three (rarely to five) times forked, rather lax, 1–1.5 mm apart at the margin, immersed, free, but in large leaves a few anastomoses may be found. Margin with a whitish thickened border at the bottom of the sinus, otherwise indistinctly thickened, stramineous to brownish, entire to very faintly and minutely erose-crenate, sometimes slightly more in sterile leaves, occasionally slightly crispate; no sterile leaf of normal size seen. *Sori* leaving the whole sinus or its proximal half free. Indusium ca. 0.5 mm wide, concolorous with the dorsal surface, not reaching the margin by 0.5–1.5 mm, reflexed and conceiled at full maturity. Sporangia ca. 185 × 138 μ; annulus with 8–10 indurated cells; spores ca. 23 30 μ, pale brown to yellow; a small number of monolete spores sometimes found intermingled, these ca. 30 × 17 μ.

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*) The writer's observations do not agree with WAGNER's figure (cited above), which shows a short basal midrib, for which he may have mistaken the extension of the sclerotic patch.

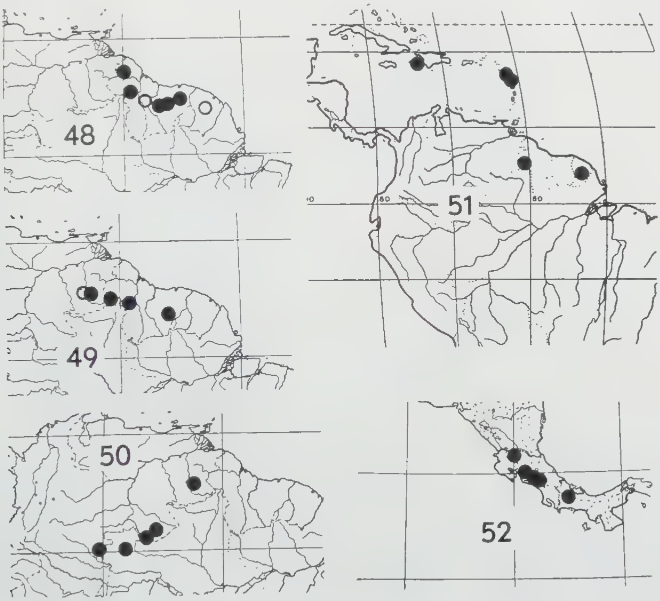
Distribution: Guayana (map 49). In forests, in moist localities, sometimes along streams, up to ca. 1000 m.

Venezuela. Bolívar: Vic. of Salto de Pacairao, n.e. of Santa Teresita de Kavanayén, Steyermark 60518 (F, NY, US); Chimantá-Massif, slopes of Toronotepuí, Steyermark 75416 (US); Mt. Roraima, Venezuelan side, Schomburgk s.n. (K).

British Guiana: Essequibo R., Appun 42 in part (B); Essequibo and Rupununi Rs., Schomburgk 533 (B, BM, BR, K, L, NY, US, W); Pacatout below the Kaieteur, Potaro R., Jenman 1394 (K, NY); without loc., Winter s.n. (C. Chr. in BM, UC), Schomburgk 367 (B, BR), Schomburgk 68 (BM, BR, C. Chr. in BM, FI, K, W).

Suriname: Tafelberg, top, Maguire 24243 (A, F, K, MO, NY, U, UC, US); ibid., id. 24817 (A, F, K, NY, U, US); without loc., Anderson s.n. (BM, Holotype).

French Guiana: without loc., Martin s.n. (BM).



Map 48: *Lindsaea sagittata.* Map 49: *L. reniformis.* Map 50: *L. cyclophylla.* Map 51: *Ormoloma imrayanum.* Map 52: *O. standleyi.*

Most closely allied to *L. cyclophylla;* the differences are discussed under that species.

Posthumus (1927) claimed to have proved that *L. reniformis* could not be separated from *L. sagittata.* His conclusion was mainly based on the fact that the basal lobes in the latter species are not always acute but may be rounded, as in the former, a fact already known to Dryander; and on an abnormal leaf of *L. sagittata,* were the leaf-apex was not developed because of damage, apparently at an early stage. It is quite clear that this is not sufficient evidence; the present author has not seen a single dubious or intermediate specimen. The only other author who reported specimens of *L. reniformis* tending towards *L.*

sagittata was Jenman (l.c., p. 72); his observations of "an occasional frond to become pointed" probably refer to leaves where the distal margin has an outstandingly protruding portion. The present author has probably seen all of Jenman's specimens and has not found any specimens of *reniformis* with pointed leaf-top.

40. **Lindsaea cyclophylla** Kramer, spec. nov. **Fig. 90, 91**

Misapplied names: *L. reniformis* auct. non Dryand.; Baker, Fl. Bras. I^2:357 (1870), in part; Wagner, Am. Jo. Bot. 39: fig. 9H (1952).

L. reniformi valde affinis, differt petiolo facie abaxiali superne usque ad cacumen angulari; lamina potius orbiculari vel in plantis juvenilibus reniformi, sporisque diplanatis.

Typus: Holt & Blake 494 from Serra Imeri, terr. Amazonas, Venezuela (US).

Rhizome short-creeping, ca. ½ mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long and 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* rather close, subdistichous, 10–20 cm long, 2–4(–6), mostly about 3 × as long as the lamina, ca. 0.6 mm in diam. at the base of the lamina, dark brown to atropurpureous, rather shining, adaxially terete in the lower third, above with lateral ridges that become narrow pale wings between which the surface is more or less flattened in the upper part, abaxially the same happens roughly halfway, the petiole thus being quadrangular in its upper part, with four often pale narrowly winged angles. The angles of the adaxial side are continuous with the marginal strand of the lamina, those of the abaxial surface extend up to or into the sclerotic patch at the base of the lamina. This patch is adaxially as in the preceding species; abaxially it is smaller, more regular in shape, mostly without a central extension but with several short ones extending not more than about 0.5 mm along the veins, giving the patch a stellate appearance. *Lamina* almost circular in large leaves, reniform or bean-shaped in small leaves of juvenile plants, chartaceous, medium green on the ventral, paler on the dorsal side, 2.5–7 cm long, 3.5–8 cm wide, 0.5–2 cm wider than long, rarely approximately isodiametric, deeply cordate (or in small leaves shallowly emarginate), the sinus 1.5–3 cm deep, reaching to about $^2/_5$ of the length of the lamina, mostly narrow, the basal lobes sometimes overlapping. Margin very evenly rounded except at the sinus, marginal thickening stramineous or pale brown, visible throughout but strongest at the base, slightly more distinctly and more irregularly erose-denticulate than in *L. reniformis*, in addition distinctly crispate-undulate, crenate in sterile leaves except in the sinus, the incisions ca. 0.5–1 mm deep, separating one or two vein-ends. Veins regularly dichotomously 3–4(–5) times forked, rather lax, ¾–1½ mm distant at the margin, immersed except for the base where they are slightly elevated just beyond the sclerotic patch; no main vein developed. *Sori* continuous to the edge of the sinus but not extending into it; indusium concolorous with the lamina, ca. 0.5 mm wide, subentire or mostly minutely erose-denticulate, not reaching the margin by 0.5–1.5 mm, reflexed and conceiled at full maturity. Sporangia ca. 160–165 × 125 μ annulus with 9 or 10 indurated cells; spores bean-shaped, very pale brownish, almost colourless, ca. 33 × 21 μ, 16?

Distribution: North-western borderlands of the Amazon basin (map 50). In forests, along creeks, on sandstone or igneous boulders, at about 600–800 m.

Brazil. Amazonas: Panuré on Rio Uaupés, Spruce 2916 (K).
Venezuela. Amazonas: Western foothills of Serra Imeri, near Salto de Huá, ca. 800 m, Holt & Blake 494 (US, Holotype; Isotypes in GH, NY, US); Cerro de la Neblina, Rio Yatua, Maguire, Wurdack & Bunting 36806 (US; juvenile).

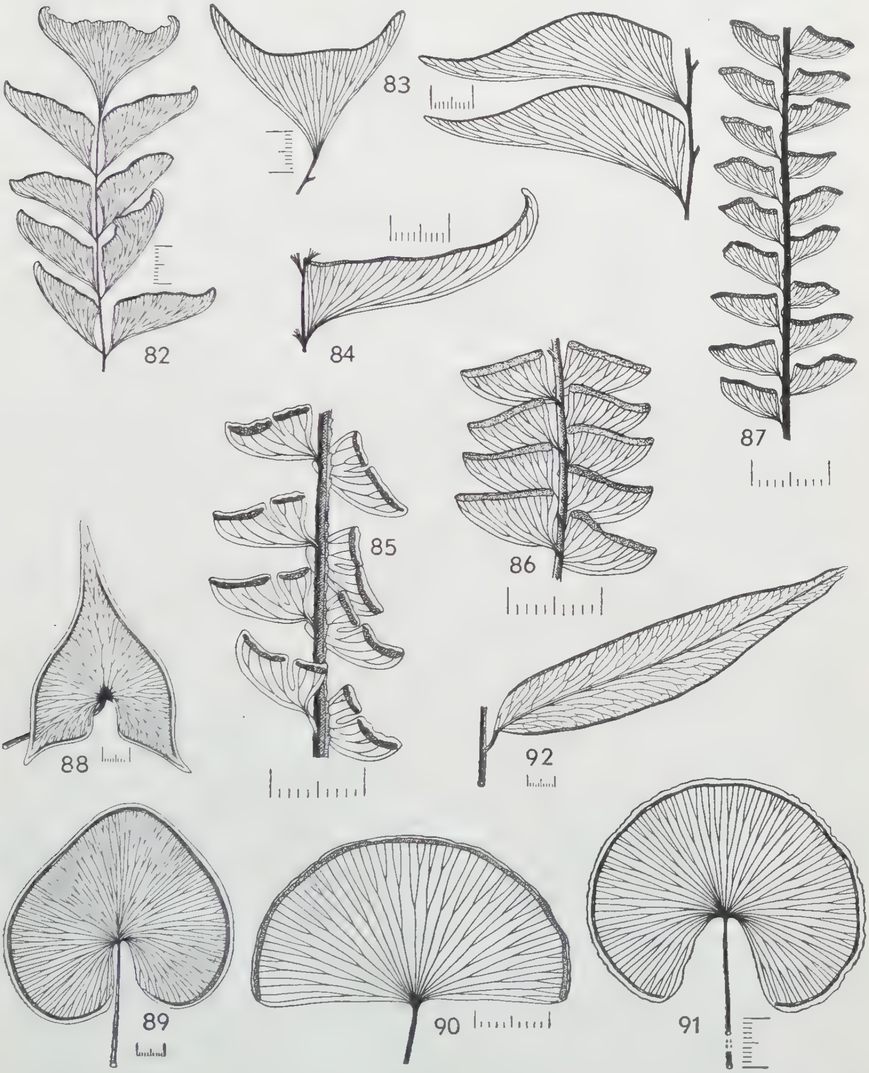


Fig. 82: *Lindsaea semilunata;* complete lamina (Appun s.n., Glaziou 12353). Fig. 83: *L. latifrons;* terminal pinnule (left) and lower pinnules from bipinnate leaf (Klug 2890). Fig. 84: *L. hemiglossa;* upper pinnule (Spruce s.n.). Fig. 85: *L. seemannii* var. *serrigera;* middle of lamina (Lehmann 737). Fig. 86: *L. pratensis;* middle of lamina (Wercklé s.n.). Fig. 87: *L. protensa;* middle of lamina (Ekman H 10243). Fig. 88: *L. sagittata;* lamina (Boschwezen 587). Fig. 89: *L. reniformis;* lamina (Maguire 24817). Fig. 90–91: *L. cyclophylla;* fig. 90: lamina of juvenile plant (Steyermark 74800); fig. 91: lamina of mature plant (Holt & Blake 494). Fig. 92: *L. macrophylla;* lateral pinna (Riedel s.n.). (Scales in mm).

Bolívar: Chimantá Massif, western sides of Apácara-tepuí, Steyermark 74663, 74800 (US).
Colombia. Vaupés: Rio Kananarí, Cerro Isibukuri, Schultes & Cabrera 15064 (US).

Closely related to *L. reniformis.* for the diffierences, see the latin description.

Sectio VI. **Paralindsaea** (Keyserling) C. Christensen, Ind. Fil. xxx (1906).

Paralindsaya Keyserling, Polypod. & Cyath. Herb. Bung. 3, 21 (1873), as subgenus of *Lindsaea.*

Leaves dimorphous, the sterile ones short, decurved, simply pinnate, always present, the fertile ones longer, erect, once or twice pinnate. Type species: *Lindsaea linearis* Swartz.

41. **Lindsaea cubensis** Underwood & Maxon, Smithson. Misc. Coll. 50:336 (1907). **Fig. 33, 71**

Type: Wright 3947, from Loma pelado, Cuba (NY!)

Misapplied name: *L. portoricensis* auct. non Desvaux; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), in part.

Petioles stramineous or reddish brown; leaves herbaceous, somewhat dimorphous; sterile leaves spreading, simply pinnate; fertile leaves erect, simply pinnate or sometimes bipinnate with conform terminal pinna; sori continuous; indusium rather wide, erose or laciniate; spores monolete.

Rhizome short-creeping, ca. 1 mm in diam.; scales almost linear, up to 1 mm long, 0.2 mm wide, with up to 4 rows of cells at the base, for the greater part consisting of 2 or 1 row only. *Petioles* rather close, adaxially shallowly sulcate, abaxially obtusely angular to rounded; often crushed, the structure not easily observed; primary rachis similar to the upper part of the petiole. *Leaves* more or less dimorphous. *Sterile leaves* with a petiole 0.5–4 cm long, ca. ¼ mm in diam.; lamina 3–7(–9) cm long, ca. ½–1½ cm wide, with 6–12 pinnules to a side, these subopposite to alternate, delicate, pale green, somewhat ascending or spreading, the lower ones widely spaced, interstices equalling their width or larger, the upper ones closer, subcontiguous; roundish or dimidiate-ovate to subtriangular, ca. 4–8 mm long and 3–6 mm wide, from as long as wide to ca. 1½ × as long as wide, subsessile, subentire to shallowly undulate-crenate, the upper margin mostly minutely erose, the inner margin often touching or even overlapping the rachis, all margins more or less equally and not strongly convex, or all but the upper straight, but little thickened; veins simple or mostly once forked, lax, their ends ca. 1 mm apart, the main vein ca. ½ mm above the lower margin. Upper pinnules little or not reduced; terminal segment large, often larger than any pinnule, ¾–1 cm long, lobed-incised at the base, confluent with one or two lateral pinnules, lanceolate to lozenge-shaped or even square, obtuse. *Fertile leaves* with a petiole (3–)6–13 cm long, ½–1 mm in diam.; lamina with one to two up to 6 cm long primary pinnae to a side, (3½–)5–18 cm long, 10–22 mm wide, with 8–25 pinnules to a side, these subopposite to alternate, pale to medium green, herbaceous, spreading or laxly ascending, the lower ones up to 3 cm apart, the upper ones gradually closer but mostly not contiguous, very variable in shape, subtriangular, dimidiate-ovate, flabellate, cuneate, or even dimidiate-tongue-shaped, ca. 6–12 mm long and 3–9 mm wide, mostly about twice as long as wide, sometimes less, subsessile to short-stalked (up to 1 mm), entire, the inner margin straight, often touching or overlapping the rachis, the upper margin convex, sometimes only near the apex, subentire to minutely erose or superficially incised, lower margin straight, convex towards the apex, the upper base truncate or mostly shortly rounded, the apex rounded; veins or once or twice forked. Otherwise as the sterile leaves. *Sori* along the upper/outer margin, also in the terminal segment; indusium greyish, ca. ½ mm wide, not reaching the margin by ¼-½ mm, mostly little or not reflexed at full maturity. Sporangia ca. 125–130 × 105 × 110 μ; annulus with 10–13 indurated cells; spores semi-elliptic to bean-shaped, medium brown, ca. 19 × 31 μ, 32?

Distribution: Western Cuba and Isla de Pinos (map 47). In pinelands and scrub, almost always along watercourses; altitude not noted.

CUBA. PINAR DEL RIO: Herradura, Shafer 427 (NY, Paratype); Los Palacios to Herradura, Shafer 11698 (NY); near El Guama, Palmer & Riley 287 (BM, C, GH, NY, US); ibid., id. 550 (BM, C. Chr. in BM, MO, NY, S–PA, Paratypes); Sierra de Cabra, Britton, Britton & Cowell 9785 (NY, US); ibid., Guane road, Britton, Britton & Gager 7290 (NY), 7222 (NY, US); east of Viñales, Ekman 18008 (G, NY, S, US). Prov.?: Loma pelado, in dense bunches under overhanging rocks, Wright 3947 (NY, HOLOTYPE; Isotypes in B, GH, K, MO, NY, S–PA, U, US).

ISLA DE PINOS: near Managua, Palmer & Riley 1060 (US, Paratype); near Nueva Gerona, Palmer & Riley 1027 (C, NY, US, Paratypes); ibid., Curtiss s.n. (NY, Paratype); La Cunagua, Britton, Britton & Wilson 14553 (F, NY, US); Swetland Ranch, San Francisco de la Piedras, Killip 34547 (US); Santa Bárbara-Mina de Oro, Killip 43866 (US); without loc., Jennings 418 (NY).

In spite of the great variability of the pinnules, this species can be easily recognized by its delicate stipes, small size, large terminal segment, and the almost universal presence of sterile leaves. The dimorphism is not absolute, as transitions between sterile and fertile leaves do occasionally occur, and leaves of the fertile shape are sometimes only incompletely fertile; but in most cases it can be readily observed. There is no obvious relative in the New World, but there is a striking resemblance to *L. linearis* Sw. from Australia, New Zealand, and New Caledonia. The latter agrees in its dimorphism, with small spreading sterile and large erect fertile leaves, in the lower pinnules being remote but not reduced, in similar pinnules and erose indusia. Points of difference are the larger and wider rhizome scales, the dark petiole and rachis, the wider indusia, always simply pinnate leaves, and trilete spores of *L. linearis*. For these reasons, *L. cubensis* is placed with misgivings in the present section, and the phytogeographical implications of the supposed relationship are not discussed at length. It may be pointed out here that a parallel case is found in the section *Tropidolindsaea*, also of the Caribbean region, whose closest relative is beyond doubt *L. viridis* from New Zealand.

Sectio VII. **Tropidolindsaea** Kramer, sect. nov.

Lamina simpliciter pinnata, pinnulis superioribus et inferioribus sensim redactis; petiolo rhachideque facie abaxiali carinatis vel angustato-rotundatis; cellulis induratis annuli pedunculum sporangii non attingentibus; sporis oblongis.

Species typica: *Lindsaea seemannii* J. Smith.

The species of this section are quite outstanding among the neotropical Lindsaeas by the lamina being gradually reduced above *and* below, the abaxially keeled or narrowed-rounded petiole and rachis, and the annulus, the indurated part of which does not reach the stalk of the sporangium, the latter character also observed in some species of *Sphenomeris*. In addition, the rhizome-scales are large and ovate or broadly lanceolate and in one species clathrate, unlike any American species, and the spores are always monolete. A related species, to be placed in an allied section, or perhaps in the same section, is *Lindsaea viridis* Col. from New Zealand. The section *Tropidolindsaea* should perhaps be raised to the rank of subgenus.

42. **Lindsaea seemannii** J. Smith, Bot. Voy. Herald 239 (1854); Hist. Fil. 268 (1875), non Carruthers, 1873. **Fig. 32**

Type: Seemann 976 from the Bay of Chocó, "Panama" (now Colombia) (BM!).

Rhizome-scales clathrate; petioles reddish to dark brown, abaxially keeled; lamina simply pinnate, linear, herbaceous; rachis abaxially keeled; pinnules ca. 2 × as long as wide, the upper margin incised; upper and lower pinnules gradually reduced; sori interrupted, mostly binerval, usually three per pinnule; spores monolete.

Rhizome short-creeping, ca. 1.5 mm in diam.; scales ovate to broadly lanceolate, acuminate, up to 2.4 mm long, 0.75 mm wide, with up to 15 rows of cells at the base, clathrate, the tangential and marginal longitudinal walls very pale, the other longitudinal and all transversal walls medium brown (fig. 5); the cells relatively regular in shape, the median ones hardly more elongate; reduced scales only in small numbers present near the rhizome-apex. *Petioles* close, very lustrous, ca. 3–8 cm long, ¾–1 mm in diam., adaxially narrow, channelled, roughly triangular in cross-section, the lateral surfaces flattish or convex. *Lamina* obtuse, ca. 15–35 cm long, two to more than five times as long as the petiole, ca. 1.5–2 cm wide, pale to brownish green, with 30 to more than 50 pinnules to a side. *Rachis* adaxially with a narrow groove with paler edges, abaxially keeled below, the keel becoming wing-like and pale in the upper ⅔ or ½ of the rachis. *Pinnules* subopposite or the upper ones alternate, the middle ones rather close but not contiguous, the lower ones gradually remote and strongly reduced, sometimes auriculiform, the upper ones gradually but not very strongly reduced, the leaf-apex rather suddenly pinnatifid with a few confluent cuneate segments. Largest pinnules ca. 10 mm long, 5–6 mm wide, in outline resembling ¼ of an ellipse, subsessile, spreading, the upper ones slightly ascending, the reduced basal ones often somewhat deflexed. Lower margin evenly convex, inner margin ± straight, often touching or slightly overlapping the rachis, lower base very shortly stalk-like, inserted on a brown protuberance of the rachis where it is easily detached but not truly articulate, upper margin incised with at least one incision 2–3 mm deep, the sinus rounded, ca. 0.5 mm wide at the margin, the lobes mostly about 2–5 mm wide, often not equal in length, their outer margins not in one line, sinuate or sometimes erose. Marginal strand almost absent, except at the extreme lower base. Veins immersed or very slightly protruding; the vein at the basiscopic side (hardly to be called a main vein) ca. 3 mm above the lower margin; lateral veins once forked, (1–)2(–4) per lobe. *Sori* laterally extending beyond the vein-ends. Indusium membranous, ca. 0.5 mm wide, sinuous-erose, mostly not quite reaching the margin, not reflexed at full maturity. Sporangia ca. 250 × 200 μ; annulus with 12-15 indurated cells (fig. 20); spores subelliptic, rather pale brownish-yellow, 50–55 × 37 μ.

a. var. **seemannii**.

Wing on the abaxial side of the rachis entire or sinuous, usually not wider than 0.1 mm; pinnules mostly with two or three incisions.

Distribution: Eastern Panamá and western Colombia; on cliffs and rocky bands, near sea-level (map 46).

Panamá. Darien: Isthmus of Darien, Seemann s.n. (US, Paratype).
Colombia. Chocó: Bay of Chocó, Seemann 976 (BM, Holotype; Isotypes in B, K, photogr. in US); between La Oveja and Quibdó, Archer 1670 (US).

El Valle: Punta Magdalena, Haught 5581 (S–PA, US); Colorada, n. shore of Buenaventura Bay, Killip & Cuatrecasas 38695 (US).

b. var. **serrigera** Kramer, var. nov. **Fig. 85**

Recedit a varietate typica pinnulis minus incisis, ala carinae faciei abaxiali rhachidis petiolique valde prominente, conspicue et irregulariter eroso-repanda vel serrata.

Typus: Lehmann 737 from Sucre, Cauca, Colombia (US).

Pinnules mostly with only one incision near the base; some sori occupying six or even eight veins; wing-like borders of the adaxial groove also irregularly erose-sinuate.

Distribution: Colombia; on banks in very moist forest, 200 m. Only known from type-collection (map 46).

Colombia. Cauca: Near Sucre, Río Dagua, Lehmann 737 (US 826432, Holotype; Isotypes in B, BM, C. Chr. in BM, G, K, LE, US).

Most closely allied to *L. pratensis*, where the differences are discussed It has nothing to do with *L. cultrata*, with which it was compared by Hooker & Baker (1868, 1874, p. 105).

43. **Lindsaea pratensis** Maxon, Am. Fern Jo. 23:73 (1933). **Fig. 86**

Type: Wercklé s.n. from Costa Rica (US).

Rhizome-scales not clathrate; petioles reddish to dark brown, abaxially obtusely keeled; lamina simply pinnate, linear, mostly coriaceous; rachis abaxially keeled below, winged above; pinnules 30–50 to a side, 1 ½–2 × as long as wide, not or hardly incised; upper and lower pinnules gradually reduced; sori continuous or rarely slightly interrupted; spores monolete.

Rhizome creeping, ca. 2 mm in diam.; scales yellowish brown, ovate to broadly lanceolate, acuminate, ca. 4 mm long and 1 mm wide, with up to 20 rows of cells at the base; the cells very irregular, those of the apex more elongate than the basal ones. *Petioles* not very close, 7–15 cm long, one half to two-thirds the length of the blade, ca. ¾ mm in diam. near the apex, rather dull, adaxially with a shallow rather broad groove or flattened below, approximately triangular in cross-section, the lateral sides convex. *Lamina* ca. 12–25 cm long, 1.5–3.5 cm wide, coriaceous or rarely chartaceous, brownish green. *Rachis* below similar to the petiole, above abaxially with a pale often very coarsely and irregularly erose-dentate wing, the borders of the adaxial groove never erose. *Pinnules* subopposite, the upper alternate, the middle and upper ones very close, contiguous or mostly somewhat overlapping (succubous), ± spreading, sessile, ca. 8–13 mm long, 5–8 mm wide, subtriangular, semi-crescent-shaped or ¼-elliptic, those of the lower ⅔ of the lamina very gradually reduced and remote, 2–5 cm apart, in the upper ⅓ of the lamina gradually reduced to the pinnatifid leaf-top. Apparently the leaves develop very slowly; in otherwise mature leaves the apex is still involute and quite immature and very often lost; perhaps the lamina develops intermittently, as in *Jamesonia*. Lower edge of pinnules straight or usually somewhat convex, inner edge more or less concave, touching or slightly overlying the rachis, lower base not stalk-like, inserted on a protuberance of the rachis as in the preceding species, upper edge straight or slightly convex or concave, the apex blunt or often slightly apiculate and upturned. All edges entire, or the upper edge with one incision up to 2 mm deep near the middle. Marginal thickening indistinct, except at the lower base. Veins immersed, mostly somewhat impressed adaxially, simple or once forked, their ends ca. ¾–1 mm apart; main vein ca. 0.2–0.3 mm above the lower margin. *Sori* along the upper margin; indusium delicate, ca.

0.4 mm wide, subentire or erose, almost equalling the margin, hardly reflexed at full maturity. No full-size sterile pinnules seen, the basal reduced ones usually incompletely fertile. Sporangia ca. 250 × 200 μ; annulus with 14–16 indurated cells; spores subelliptic, pale brownish-yellow, ca. 52 × 39 μ.

Distribution: Endemic in Costa Rica (map 46). On wet, open, grassy bank, (1400?–) 2000–2400 m.

Costa Rica. Cerro de las Caricias, north of San Isidro, Heredia prov., Standley & Valerio 52245 (GH, US, Paratypes); Carillo region, Lankester s.n. (BM); garden at San José, originally from La Palma, Wercklé s.n. (US, Paratype); without exact loc., Wercklé s.n. (US, Holotype).

Most closely allied to *L. seemannii*, from which it differs by the non-clathrate scales, closer and firmer pinnules, and mostly not incised upper margin. *L. protensa*, which is more remotely related, has smaller, thinner, more numerous pinnules.

44. **Lindsaea protensa** C. Christensen, Kungl. Sv. Vet.—Akad. Handl. Ser. III, 16 (2): 45 (1937), pl. XI fig. 1–3. **Fig. 87**

Type: Ekman H 10243 from Massif de la Hotte, Hispaniola (C. Chr. in BM!).

Rhizome-scales not clathrate; petioles reddish brown, abaxially narrowed-rounded; lamina simply pinnate, linear, herbaceous; pinnules ca. 80–100 to a side, ca. 1½ × as long as wide, not over 8 × 5 mm, entire; upper and lower pinnules gradually reduced; sori continuous; spores monolete.

Rhizome creeping, ca. 2–3 mm in diam.; scales yellowish-brown, broadly lanceolate, acuminate, up to ca. 3 mm long, ¾ mm wide, with about 16 rows of cells at the base. *Petioles* rather close, ca. 3–6, mostly about 4 cm long, ¾–1 mm in diam., rather shining, adaxially with a sharply delimited flat portion. *Lamina* elongate, ca. 35–80 cm long, 1–2 cm wide near the middle, pale green. *Rachis* similar to the petiole. *Pinnules* subopposite, the upper ones alternate, spreading, the upper ones ascending, the largest rather close but not contiguous, 5–8 mm long, 3–5 mm wide, in the lower half or one-third of the lamina gradually reduced and farther apart, the lowest ca. 2 cm apart, in the upper third of the lamina also gradually reduced, a few linear segments connected by a wing; no well-developed terminal segment present, the leaf-top incurved, immature, or missing in most leaves which apparently develop quite slowly, perhaps intermittently. Largest pinnules obliquely triangular to ¼-elliptic in outline; lower margin convex, inner margin S-shaped to straight, ± parallel to the rachis, upper edge straight, slightly concave, or with a shallowly concave portion in the basal half, often somewhat erose-sinuate, apex bluntish to subacute, lower base cuneate, with a stalk-like portion of ca. ½ mm, with hardly any trace of an articulation as in the two preceding species, but the dark colour of the rachis suddenly fading at the base of the pinnules. Veins immersed but readily visible, once or twice forked, their ends ca. ½ mm apart; main vein close to the lower edge; marginal thickening externally not visible. *Sori* along the upper margin; indusium delicate, ca. 0.4 mm wide, sinuate-erose, equalling the margin, hardly reflexed at full maturity. No full-size sterile pinnules seen, reduced lower pinnules usually at least incompletely fertile. Sporangia ca. 230 × 185 μ; annulus with 15–16 indurated cells; spores subelliptic, pale brownish-yellow, ca. 45–50 × 37–41 μ, 16?

Distribution: Endemic in the south-western peninsula of Hispaniola (map 46). On lateritic soil, 150 and 900 m.

Hispaniola. Haïti: Massif de la Hotte, western group, Jérémie, between La Source Chaude and Source Cahouane, Ekman H 10243 (C. Chr. in BM, Holotype;

Isotypes in B, GH, K, NY, S, UC, US); ibid., near Lopineau, Ekman H 10402 (B, C, F, S, Paratypes).

Not as close to *L. pratensis* as Christensen supposed, but apparently most closely related to that species. The abaxially almost terete petiole and rachis and the small very numerous pinnules distinguish it quite readily.

Subgenus B. **Schizoloma** (Gaud.) Hooker, Spec. Fil. I:219 (1844). *Schizoloma* Gaudichaud, Ann. sci. nat. 3:507 (1824), as genus.

Veins anastomosing, without included veinlets; lamina simply pinnate, with large equal-sided pinnae with a median main vein, or, when bipinnate, with large undivided pinna-apices; sori continuous.

Type species: *Schizoloma billardieri* Gaudichaud (= *Lindsaea ensifolia* Swartz).

45 **Lindsaea macrophylla** Kaulfuss, Enum. 218 (1824); Sprengel, Syst. Veget. IV:79 (1827); Kunze, Anal. 37 (1837), pl. 25; Hooker, Ic. Fil. II t. 193 (1837); Hooker & Bauer, Gen. Fil. t. 63 B (1840); Hooker, Spec. Fil. I:220 (1844); Klotzsch, Linnaea 20:445 (1847); Kunze, Bot. Zeit. 8:404 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868); 2nd ed. (1874) 112; Baker, Fl. Bras. I²: 358 (1870), pl. 42 fig. 1; Christ. Farnkr. d. E. 298 (1897); Jenman, W. Ind. Gui. F. 72 (1899). **Fig. 92**

Type: Chamisso (?) s.n. from French Guiana, not seen (prob. P). Homotypic synonym: *Schizoloma macrophyllum* (Kaulfuss) Presl, Tent. Pterid. 132 (1836); J. Smith, Hist. Fil. 271 (1875); Kuhn, Chaetopt. 26 (1882); Diels, N. Pfl. I⁴:219 (1902); Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930).

Lamina simply pinnate, chartaceous; pinnae almost equal-sided, broadly lanceolate, the upper and the terminal one not reduced; veins reticulate; sori continuous, interrupted at the pinna-apex; spores monolete.

Rhizome not seen. *Petioles* (only one complete specimen seen) up to 52 cm long, rather stout, 1.5–2 mm in diam. near the apex, castaneous to greyish-brown, rather shining, adaxially sulcate, with sharp, often somewhat paler angles, abaxially obtusely angular below, sharply angular above, there flattened or sulcate. *Lamina* ovate in outline, 30–35 cm long, medium green to olivaceous, paler on the dorsal side, with 3–4 pinnae to a side and a conform terminal one. *Rachis* similar to the upper part of the petiole, but adaxially flattened with raised borders, not concave. Axillary cushions indistinct, slightly swollen and discoloured. *Pinnae* alternate or subopposite, ascending under an angle of ca. 30–60°, rather wide-spaced to moderately close, the lower ones 5–6 cm apart, the upper ones closer, not contiguous, 13–17 cm long, 3–4 cm wide, 4–5 × as long as wide, broadest in the middle or mostly in the lower third, the terminal pinna always relatively broadest, with a stalk of 2–3 cm, lateral pinnules with a stalk-like base of ca. ½ cm, the basiscopic half often more strongly convex than the acroscopic, the cuneate base also unequal, the leaf-tissue extending farther down on the acroscopic side, in addition often somewhat folded over at the basiscopic side; base of the terminal pinna equal or almost so. All pinnae gradually narrowed from the broadest point, the apex often somewhat acuminate, the very top blunt or subacute. Margins with a strong, often revolute, entire, stramineous strand that extends around the apex (the sterile apex of the pinnae figured as being serrate in Hooker & Bauer's plate). Veins immersed or very slightly elevated, very oblique near the midrib, less so towards the margin, 3–5 times forked, usually with one or two anastomoses between midrib and margin, the meshes exappendiculate; vein-ends very irregularly spaced, ca. 1–3 mm apart. Midrib strong, approximately median, slightly flexuose, percurrent, abaxially elevated, stramineous, adaxially immersed, except near the base. *Sori* along both margins from about 1 cm above the base, interrupted in the apex, where the receptacle may be nevertheless continuous; no sterile pinnae seen. Indusium greyish, entire, ca. 0.4 mm wide, not reaching the margin by approximately its own width, strongly reflexed and conceiled at full maturity. Sporangia ca. 140 × 115 μ; annulus with ca. 10–14 indurated cells; spores bean-shaped, hyaline, almost colourless, ca. 23 × 27 μ.

Distribution: North Brazil and French Guiana, also reported from other regions, but probably confused with species of *Adiantum*. No ecologidal data extant.

BRAZIL. PARÁ: Bay of Esperara (or Esperança), Riedel s.n. (GH, K, U, W, fragment, prob. of this coll., in F).

This very remarkable and apparently extremely rare species has no relatives in the Western Hemisphere. It is most closely allied to *L. ensifolia*, which is widespread in the tropics of the Eastern Hemisphere, and the only species occurring on the African continent. The two species agree in such diverse characters as leaf-pattern, unequal pinna-bases, venation, structure of the petiole, etc.; but *L. macrophylla* has broader pinnae, smaller sporangia, and monolete spores.

Most specimens in herbaria determined as *Lindsaea macrophylla* belong to *Adiantum dolosum* Kunze. HOOKER (1844, p. 220/221) admitted to have made a similar mistake; KUNZE (1850, see above) believed Hooker-Bauer's plate to represent the same species, but in the present author's opinion this is not certain. Incidentally, the plate incorrectly shows the veins to be free. The specimen from Cumana, Venezuela, cited by Klotzsch and Knuth (see above) (Moritz 155), not seen by the author, may also be an *Adiantum*. On the other hand, it is hardly likely that *Kaulfuss'* type itself is an *Adiantum*, not a *Lindsaea*, although the author cannot confirm this on the base of his own observations.

SPECIES OF UNCERTAIN STATUS

Lindsaea falciformis Hooker, Spec. Fil. I:208 (1844), t. 64 B; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 104; Baker, Fl. Bras. I²:351 (1870); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 72 (1899); Posthumus, Fl. Surin. Suppl. 71 (1928); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:74 (1948).

Type: Schomburgk s.n. from Mt. Roraima, British Guiana (K!, Isotype in BM).

This species is unlike any species from the Guianas except *L. surinamensis;* from this it differs by smaller, more numerous pinnules which are more falcate, but it may be an abnormal form of that species. It has never again been collected.

Lindsaea mazaruniensis Jenman, W. Ind. Gui. F. 75 (1899); Posthumus, Fl. Surin. Suppl. 76 (1928).

Type: Jenman 2265 from the falls of the Mazaruni River, British Guiana (K!); a specimen which may be a duplicate in NY.

Not unlike a bipinnate specimen of *L. lancea*, but differing by dark, abaxially quite terete primary rachis, more strongly intramarginal sori, and much more rounded pinnules which are often broadest near the apex, not unlike those of *L. botrychioides*. Almost all sporangia (in the K specimen) abortive, the few normal ones with abortive spores. Another specimen: Appun 831 from British Guiana (K) is ± similar, but simply pinnate, with more elongate pinnules; the sporangia are normal, but the spores also abortive. Probably a hybrid; one of the parents almost certainly *L. lancea*, the other perhaps *L. divaricata*.

Lindsaea montana Fée, 11^{e} mém. 17 (1866), t. 6 fig. 2; non Copeland, 1905.

Type: L'Herminier s.n. from Guadeloupe (P!).

Almost all authentic specimens, including the type, are mixtures of *L. guianensis* ssp. *guianensis* and the form described above as *L. quadrangularis* ssp. *antillensis*, with which the name has almost universally been associated. Neither Fée's description nor his plate make it possible to decide to which of the two forms the name should preferably be applied; therefore it seems best to regard it as a *nomen confusum*. For more complete citations see under *L. quadrangularis* ssp. *antillensis*.

Lindsaea pumila Klotzsch, Linnaea 18:545 (1844); Hooker, Spec. Fil. I:209 (1844); Kunze, Linnaea 21 :225 (1848); Kunze, Bot. Zeit. 8:325 (1850); Jenman, W. Ind. Gui. F. 73 (1899); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930); not of C. Christensen, Dansk Bot. Ark. 6:97 (1929), nor *L. pumila* (Brack) Hooker & Baker, Syn. Fil. 1st ed. 113 (1868), which is *Diellia erecta* Brack. f. *pumila* (Brack.) Wagner.

Type: Schomburgk 1138 from British Guiana (B!).

The type-specimen has small rhizomes with small scales like those of *L. lancea* and simply pinnate leaves up to 11 cm long; the petioles are dark, sharply quadrangular almost to the base, the pinnules ca. 10–15, not unlike those of *L. lancea* var. *remota* but firmer, up to 9 × 5 mm, the terminal segment broadly lanceolate, free or connected with 1 or 2 lateral ones; the indusia are continuous, entire or subentire, 0.4–0.5 mm wide, almost reaching the margin. Schomburgk 47 from Mt. Roraima, British Guiana (BM) is similar. This is probably a depauperate form of some other species, but it is impossible to say of which. Posthumus referred it to *L. guianensis* which is, however, not close. CHRISTENSEN (l.c.) referred to the same species a specimen from Taracuá, Amazonas, Brazil, Roman nr. 26 (C. Chr. in BM, S-PA); this differs by the abaxially terete lower half of the petiole, thinner, more rounded pinnules, and narrower erose indusia. A third collection referred to *L. pumila* by Christensen is Spruce 3064 (B, BM, BR, G, K, L, LE, W) from San Carlos, Rio Negro, Amazonas, Venezuela. This is approximately intermediate between the two collections just described, but the pinnules are more strongly reduced above, confluent with a small terminal segment, and the indusia are ca. 0.5 mm wide and strongly erose-denticulate; a very similar specimen is

Baldwin 3507 (US) from the junction of Rio Uaupés with Rio Negro, Amazonas, Brazil, also von Lützelburg 22238 (M) from São Felippe, Rio Negro, and id. 22280 (M) from Marabitana, Rio Negro. These specimens represent perhaps an undescribed species. Steyermark 58095 (F, MO, NY, US) from Mt. Duida, Amazonas, Venezuela, differs by narrower, less erose indusia, larger terminal segment, and often wing-like ridges on the petiole and rachis; von Lützelburg 22529 (M, NY, UC) from Cururú, Rio Ayarí, and id. 22679 (M) from Tunuý, Rio Içana, both Amazonian Brazil, are similar but have narrow erose indusia with erose fertile margin and strongly wing-like angles of the axes.

Unnamed forms

Of the comparatively very few specimens which the author has not been able to determine, the following are discussed because they may represent new taxa.

Two collections from Venezuela: Tate 430 (K, NY, US) from Mt. Duida, Amazonas, and Maguire, Wurdack & Bunting 37158 (US) from Cerra de la Neblina, Río Yatua, Amazonas, belong to a form allied to *L. klotzschiana*, differing by abaxially terete petioles, firmer texture, and darker colour; in general habit they are not unlike more amply bipinnate forms of *L. stricta* var. *jamesoniiformis*. The spores are trilete, most of them abortive, a few giant spores and some monolete ones were observed in the same sorus with the others; all this points to hybrid origin. A third specimen: Steyermark & Wurdack 637 (US) from Torono-tepuí, Chimanta Massif, Bolívar, Venezuela, with normal spores, is more like *L. klotzschiana* and is perhaps a backcross with that species which is almost certainly one of the parent-species. The author cannot suggest which would be the other one.

Steyermark 59409 (F, MO, NY, US) from the Gran Sabana, Bolívar, Venezuela, is intermediate between *L. schomburgkii* and *L. portoricensis;* the leaves are simply pinnate or bipinnate, with small pinnules, the upper ones reduced, but the veins are elevated, the texture coriaceous, and there is small terminal pinnule shaped as in *L. schomburgkii.* The spores are dark and wrinkled, apparently abortive, and hybrid origin is very likely, *L. schomburgkii* being probably one of the parent-species, the other perhaps *L. portoricensis.*

Steyermark 75665 (U, US) from the Chimantá Massif, Bolívar, Venezuela, has pinnules and pinna-apices not unlike those of small forms of *L. arcuata;* the petioles are stramineous to fawn, very stout, and abaxially terete, the secondary rachises are on the abaxial side more like those of *L. portoricensis.* The spores are trilete, pale yellowish. Presumably a new species, but hardly sufficiently distinct to be described on the base of only one collection.

Two collections of von Lützelburg from northern Amazonas, Brazil: 23605 (M, NY) from Varadoura, Iutica, R. Uaupés, 23674 (M) from Uapuý, R. Ayari, and a third, 23826 (M) from the Colombian side of R. Uaupés near Iutica almost certainly represent a new species. The leaves are rather long, simply pinnate, the pinnules are not unlike those of *L. hemiptera*, but the upper part of the dark brown petiole is sharply quadrangular, and the angles of the abaxial side of the rachis are pale and somewhat wing-like. The spores are trilete, pale yellowish-brown. As there is not a single full-grown leaf with a complete apex, its relationships remain uncertain, and it cannot be described here as new. Rosenstock annotated all sheets "*Lindsaya quadrangularis* Raddi v. *amazonica* Ros. n.v. (an spec. propr.)", a name that was never published; fortunately, because there is certainly no close relationship to *L. quadrangularis*.

Names of uncertain application

Lindsaea caudifera Fée, Gen. Fil. 106 (1852). Type: L'Herminier s.n. from Guadeloupe (P? not seen). Not recognized.

Lindsaea consanguinea Fée, 11ᵉ mém. 16 (1866). Two collections cited; the first, L'Herminier s.n. from Guadeloupe, is shown on pl. 6 fig. 3 of the above-cited work. It is probably a form of *L. lancea* with reduced upper pinnules and a small terminal segment, but may also represent *L. quadrangularis* ssp. *antillensis*. The authentic specimen has not been examined. The second collection, Luschnath 22 from Bahia, Brazil (B, MO!) belongs to *L. lancea* var. *lancea*.

Lindsaea falcata Dryander var. *subrotundifolia* Jenman, W. Ind. Gui. F. 74 (1899). No type specimen, or any other specimen, cited. Belongs perhaps to *L. lancea* var. *elatior*, or possibly to *L. schomburgkii*.

Lindsaea guianensis (Aubl.) Dryander var. *venosa* Jenman, W. Ind. Gui. F. 77 (1899). "In the forest near the Kaieteur Savannah", British Guiana. No specimen seen. Said to be well marked by the interrupted sori. Perhaps an incompletely fertile specimen of *L. portoricensis*.

Lindsaea ripidoteris Kunze, Bot. Zeit. 8:328 (1850). "fl. Bras. ined.", not typified. Kunze compared it with *L. flabellulata*. Perhaps a sterile specimen of *L. stricta*.

Lindsaea serrata Goldmann, Nova Acta Leop. 16 Suppl. 2:464 (1843). Type from Mt. Corvocado near Rio de Janeiro, "ad Aquaeductum", not seen. The description is most incomplete, apparently a sterile specimen, perhaps of *L. quadrangularis*.

Excluded species

L. aculeata (L.) Mettenius, Ann. sci. nat. IV, 15:65 (1861). – *Odontosoria aculeata* (L.) J. Smith, Cult. Ferns 67 (1857).

L. clavata (L.) Mettenius, Ann. sci. nat. IV, 15:64 (1861). – *Sphenomeris clavata* (L.) Maxon, Jo. Wash. Acad. Sci. 3:144 (1913).

L. colombiana (Maxon) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928). – *Odontosoria colombiana* Maxon, Contr. U.S. Nat. Herb. 17 (2):165 (1913).

L. divaricata (Schlecht. & Cham.) Mettenius ex Kuhn, Jo. Bot. 15:231 (1877), non Klotzsch 1844. – *Odontosoria schlechtendalii* (Presl) C. Chr., Ind. Fil. 209 (1906).

L. fumarioides (Swartz) Mettenius, Ann. sci. nat. V, 2:217 (1864). – *Odontosoria fumarioides* (Swartz) J. Smith, Hist. Fil. 264 (1875).

L. imrayana (Hooker) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928). – *Ormoloma imrayanum* (Hook.) Maxon, Proc. Biol. Soc. Wash. 46:144 (1933).

L. (?) *Killipii* Maxon, Contr. Gray Herb. 165:74 (1947). – *Sphenomeris killipii* (Maxon) Kramer, Acta Bot. Neerl. 6: 153 (1957).

L. Michleriana Eaton, Mem. Amer. Acad. n.s. 8:213 (1860). – *Pleuroderris michleriana* (Eaton) Maxon, Jo. Wash. Acad. Sci. 24:550 (1934).

L. panamensis (Hooker) Mettenius, Fil. Lips. 105 (1856). – *Dictyoxiphium panamense* Hooker, Gen. Fil. t. 20 (1840).

L. schlechtendalii (Presl) Christ, Farnkr. d. E. 296 (1897). – *Odontosoria schlechtendalii* (Presl) C. Chr., Ind. Fil. 209 (1906).

L. sectorifolia Goldmann, Nova Acta Leop. 16 suppl. 1:464 (1843). – Not Lindsaeoid; according to C. Christensen, Ind. Fil. 397 (1906) *Adiantum flabellulatum* L.

L. (?) *spathulata* Maxon, Contr. Gray Herb. 165:74 (1947). – *Sphenomeris spathulata* (Maxon) Kramer, Acta Bot. Neerl. 6: 153 (1957).

L. uncinella (Kunze) Krug, Engl. Bot. Jb. 24:92 (1897) (perhaps antedated by Christ, Farnkr. d. E. 297, 1897). – *Odontosoria uncinella* (Kunze) Fée, Gen. Fil. 326 (1852).

4. ORMOLOMA

Ormoloma Maxon, Proc. Biol. Soc. Wash. 49:143 (1933); Christensen Man. Pterid. 534 (1938); Copeland, Gen. Fil. 55 (1947).

Davallia J. E. Smith; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 88; Baker, Fl. Bras. I²:343 (1870), in part.

Lindsaea Dryand.; Pérez Arbeláez, Bot. Abh. Goebel 14:53 (1928), in part.

Rhizome long-creeping, with a Lindsaeoid protostele provided with a large internal phloem-strand. Scales ovate or lanceolate. Leaves not very close, subdistichous; petiole and rachis dark. Lamina simply pinnate, with a conform terminal pinna; pinnae non-articulate, petiolulate, lanceolate, crenate, approximately equal-sided, with a median main vein and free furcate secondary venation. Sori terminal on the veins or extending slightly along the vein-ends which may run parallel to the margin for a short distance; indusium semi-circular or semi-ovate, fixed at its base, otherwise free, opening outwardly; sporangia numerous, the head up to ca. 200 μ long, annulus with 10–14 indurated cells which reach the stalk; spores trilete.

Two species in Central and northern South America.

Type species: *Ormoloma imrayanum* (Hooker) Maxon (*Saccoloma Imrayana* Hooker in Kunze).

Key to the species:

1. a. Petiole atropurpureous to blackish; sori mostly 1½–2 mm long; scales lanceolate, up to 2½ × 0.6 mm . . . .
1. O. *imrayanum* (West Indies, Guiana)

b. Petiole castaneous to dark reddish brown; sori ½–1 mm long; scales ovate to lanceolate, up to 1½ × 1 mm . . . .
2. O. *standleyi* (Costa Rica, Panamá)

1. **Ormoloma imrayanum** (Hooker) Maxon, Proc. Biol. Soc. Washington 46:144 (1933); Christensen, Kgl. Sv. Vet.-Akad. Handl. 3e ser. 16 (2):44 (1937); Copeland, Gen. Fil. 55 (1947).

Basionym: *Saccoloma Imrayana* Hooker in Kunze, Farrnkr. I:86 (1841/42); Hooker, Gen. Fil. t. 58 B (1839), nom. nud.; J. Smith, Hist. Fil. 260 (1875); Diels, N. Pfl. I²:211 (1902); Duss, Fl. Crypt. Ant. franç. 73 (1904); Bonaparte, Notes Ptéridol. VII:342 (1918); Knuth, Fedde Rep. Beih. 43 (1):29 (1926); Posthumus, Fl. Surin. Suppl. 68 (1928); Domin, Pterid. Domin. 62 (1929), pl. VI fig. 2; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930); Stehlé, Caribb. For. 4 (2):93 (1943); Hodge, Lloydia 17 (2):103 (1954).

Type: Imray 84, Couliabon Mountain (= Morne Anglais?), Dominica (K!)
Homotypic synonyms: *Davallia Imrayana* (Hooker) Hooker, Spec. Fil. I:171 (1844), t. 49 A; Klotzsch, Linnaea 18:544 (1844); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 90; Baker, Fl. Bras. I^2:347 (1870); Krug in Urban, Engl. Bot. Jb. 24:90 (1897); Jenman, W. Ind. Gui. F. 66 (1899).
Humata ? Imrayana (Hooker) Moore, Ind. Fil. I:xcii (1857).
Acrophorus Imrayanus (Hooker) Moore, Ind. Fil. II:295 (1861).
Schizoloma Imrayanum (Hooker) Kuhn, Chaetopt. 26 (1882).
Lindsaya Imrayana (Hooker) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928), fig. 33 a–g.

Rhizome rather long-creeping, branched, 1–2½, mostly 2 mm in diam.; scales narrowly to broadly lanceolate, acuminate to long-acuminate, up to 2½ mm long and 0.6 mm wide, with up to 12 rows of cells at the base. *Petioles* rather close, ½–1 cm apart, sometimes less, ca. 10–30 cm long, ⅔–1½ × the length of the lamina, diam. 1–1½ mm at base of lamina, atropurpureous to blackish, shining; adaxial side channelled almost to the base, abaxial side bluntly angular above, gradually less so downwards, subterete at the base. *Lamina* simply pinnate, 9–36 cm long, 6–14, mostly about 10 cm wide, truncate-ovate to broadly lanceolate in outline, herbaceous, dark green at the ventral, paler at the dorsal side, with 2–10 lateral pinnae and a conform terminal one. *Rachis* similar to the upper part of the petiole, abaxially sharply quadrangular and occasionally shallowly sulcate in its upper part. *Pinnae* alternate, the basal ones mostly subopposite, lanceolate, 4–8½ cm long, 11–19 mm wide, ca. 4 × as long as wide, rarely less, 1½–4 cm apart, laxly ascending; upper pinnae but little reduced, ca. ⅔ the size of the lower ones, somewhat closer. All pinnae with a short stalk, which is ca. 3 mm long in the lower, ca. 1 mm in the upper ones; the dark colour of the rachis rather abruptly fading in the base of the stalk. Base of pinnae unequal, the lower base narrowly cuneate or slightly excavate, passing gradually into the lower margin, the upper base more broadly cuneate to almost truncate, passing into the upper margin by the way of a shortly rounded to almost angular portion; the stalk at the upper side winged to the base or almost to the base, unwinged at the lower side. Pinnae gradually narrowed from just above the base to the apex which is sometimes acuminate but blunt at the extreme end. Lower half of pinnules mostly a little wider than the upper, the lower margin more convex in its basal part, rarely the whole pinna is somewhat falcate-upcurved. Terminal pinna with a longer stalk (1–2 cm), mostly larger than the adjacent lateral pinna, sometimes confluent with a reduced pinna at its base, mostly slightly curved to the side opposite the highest lateral pinna. Margins of pinnae except at the narrowed base crenate, the incisions regular, ½–1 mm deep, alternating with the ends of the veins, the teeth rounded, sometimes slightly oblique, or flattened; margins of sterile pinnules, which are uncommon, similar. Thickened strand of the margin very inconspicuous. Axillary cushions not seen. Midrib almost median, percurrent, slightly flexuose, somewhat raised and stramineous at the dorsal, very slightly raised and channelled at the base of the ventral side. Lateral veins immersed, oblique, once or rarely twice forked, very lax, their ends 1½–3 mm apart at the margin. *Sori* terminal on the veins in a line that does not quite extend to the top of the pinna; indusia inserted somewhat below the level of the incisions, semi-circular or semi-elliptic, fixed at the flattish or somewhat concave base, entire, (¾–)1½–2 mm long, ½–¾ mm wide and about as far from the edge, hardly reflexed at full maturity, but the sporangia bulging from under its margin. Sporangia ca. 205 × 160 μ, annulus with 12–14 indurated cells; spores trilete, very pale brown, ca. 27–30 μ.

Distribution: Hispaniola, Guadeloupe, Dominica, and Guianas. (Erroneously reported from Costa Rica by HODGE (1954) and others) (map 51). In moist forests, from 750 to 1225 m (DOMIN 1929).

Hispaniola. Haïti: Massif de la Hotte, Ekman H 7425 (US).
Guadeloupe: Duss 4176 (MO, NY, US); Mazé 612 (K); Husnot 269 (BM, G, K, M); L'Herminier 167 (G, GH, K); L'Herminier s.n. (BM, C, G, K, L, MO, NY, UC, US).
Dominica: F. E. Lloyd 881 (NY, US); Hodge 2279 (GH, NY, US); Imray 84 (K, Holotype).
British Guiana: Mt. Roraima, Im Thurn 120 (BM, K, US); ibid., Appun 1144 (K).
French Guiana: Rivière St. Louis, Leprieur 117 (GH, US).

2. **Ormoloma standleyi** Maxon, Proc. Biol. Soc. Washington 46:157 (1933).

Type: Standley & Valerio 50039, Yerba Buena, prov. Heredia, Costa Rica (US!).

Rhizome long-creeping, sparingly branched, 1½–2 mm in diam.; scales broadly ovate and obtuse or subacute to lanceolate and acute, up to 1½ mm long and 1 mm wide, when broadly ovate with up to 25 rows of cells at the base. *Petioles* rather close, ½–2 cm apart, 9–24 cm long, diam. 1 mm at base of lamina, castaneous to dark reddish brown, shining; adaxial side angular and channelled almost to base, the borders not discoloured, abaxial side also sharply angular, or bluntly below, subterete only at the very base. *Lamina* simply pinnate, 9–24 cm long, usually as long as the petiole, 5–10 cm wide, truncate and broadly lanceolate in outline, herbaceous, dark green on the ventral, paler on the dorsal side, with 7–11 lateral pinnae and a conform terminal one. *Rachis* similar to the upper part of the petiole, the edges of the adaxial groove often pale. *Pinnae* alternate or the lower ones subopposite, lanceolate, often more elongate than in *O. imrayanum*, 2.5–7 cm long, 7–13 mm wide, 3–6½ × as long as wide, ca. 2–4 cm apart, laxly ascending; upper pinnae often considerably reduced, gradually closer. All pinnae with a short stalk, 3–4 mm long in the lower, 1–2 mm in the upper ones; the dark colour of the rachis fading in this stalk. Base of pinnae mostly, not always, less unequal than in the preceding species, the upper base being usually more narrowly cuneate, the leaf-tissue of the upper base decurrent as a narrow wing on the stalk. Top of pinnae often long acuminate, the very end blunt or subacute. Structure of leaf-top, pinnae, and venation as in the preceding species, but the basal veins not rarely twice or even three times forked. Incisions of the margin ca. 1½–2 mm apart, very shallow, ca. ½ mm deep, the teeth rounded. *Sori* as in the preceding species; indusia semi-circular or semi-elliptic, entire, ½–1 mm long, ca. ½ mm wide and as far from the margin, often reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ, annulus with 10 or 11 indurated cells (fig. 19); spores trilete, very pale brown, ca. 23–27 μ.

Distribution: Costa Rica and western Panamá (map 52). In moist forests at 1400–1800 m, terrestrial or epiphytic, probably on mossy tree trunks and stumps.

Costa Rica: Navarrito, in forest, Lankester 755 (BM, S-PA, US, Paratypes); La Palma, A. & C. Brade 51 (Rosenstock-exs. 146) (M, NY, S–PA, UC); south of Cartago, Maxon 514 (NY, US, Paratypes); near El Copey, Cordillera de Talamanca, L. O. Williams & Allen 16485 (US); Orosi, Kupper 762 (M); Cerro de las Lajas, north of San Isidro, Standley & Valerio 57434 (US, Paratype); Yerba Buena, north-east of San Isidro, id. 50039 (US, Holotype); without exact loc., Cooper s.n. (K, US, Paratypes).
Panamá: Cordillera above El Boquete, Chiriquí prov., Killip 5267 (BM, S–PA, US, Paratypes).

The two species are very closely allied. The genus *Ormoloma* is outstanding among the Lindsaeoid ferns by the highly simplified leaf-pattern but strictly uninerval sori, a condition otherwise approached among the members of this group only by *Tapeinidium pinnatum*. Its closest ally seems to be *Lindsaea;* but the author is unable to suggest to which group or species of that genus it is closest.

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THE DISPERSAL OF PLANTS BY BATS (CHIROPTEROCHORY)

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('s Gravenhage)

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A. The zoological aspect

The bats which play a role in the dispersal of plants belong to two different groups, a) the *Phyllostomidae*, a family of the *Microchiroptera* of which three subfamilies deviated from the general habits of this suborder and specialized in this direction and b) the whole suborder of the *Megachiroptera*. The first group lives in the warmer parts of the New World, the second in those of the Old World.

The ecology of the *Megachiroptera* has recently been reviewed by Eisentraut (1945) from the zoological point of view, so that I may refer to his compilation for this aspect. Of special importance for our purpose is his distributional map, reproduced here in part as Fig. 1. It embraces the group of the *Macroglossinae* (nectar feeders), which is here of no interest, and the *Pteropinae*, on the whole true fruit-eaters, though some of its members also have a tendency towards nectar feeding. The distributional area of the *Pteropinae* is larger than that of the *Macroglossinae*.

The biology of the vegetarian members of the above mentioned three sub-families of the *Microchiroptera* (the *Stenoderminae*, *Phyllonycterinae* and *Glossophaginae*, which seem to be independent lines of evolution), is less clear and contains many debatable points, which should further be studied. I refer to Allen (1940) (p. 100–105). The distribution includes the tropical mainland and the West-Indies.

Allen mentions transitional forms, which consume fruits as well as insects, and speculates on the way the diet may have changed.

Just as the nectarivorous bats from the Old and the New World, the fruit bats from the two regions have the same taste. That fruits serving as food for one group are also suitable to the other appears from observations on plants introduced from one area into the other.

The influence of bats on fruits (c.f. p. 300) may be a rather ancient one that has brought about fundamental changes. The oldest known megachiropteron seems to date from the Upper Oligocene.

Further remarks on the biology of fruit bats will be reserved for the following chapters in which they will be discussed in relation to the fruits on which they feed.

B. The role of bats in dissemination

In botanical literature some appreciation of the significance of bats for dissemination is found in the writings of authors with tropical experience. Botanists with Europe-centric concepts, however, tend to neglect the interdependence.

The work of Sernander (1927) though in other respects so thorough may be quoted as an example of this onesidedness. He mentions under "Synzoic seed dispersal" only glirochory and myrmecochory i.e. dissemination by resp. squirrels and ants. The recently published general work of Müller (1955) on seed dispersal entirely ignores bats and tropical relations. Even Guppy, a field botanist with a lifelong interest in tropical seed dispersal, shows a peculiar disregard of bats, as we shall see (p. 310).

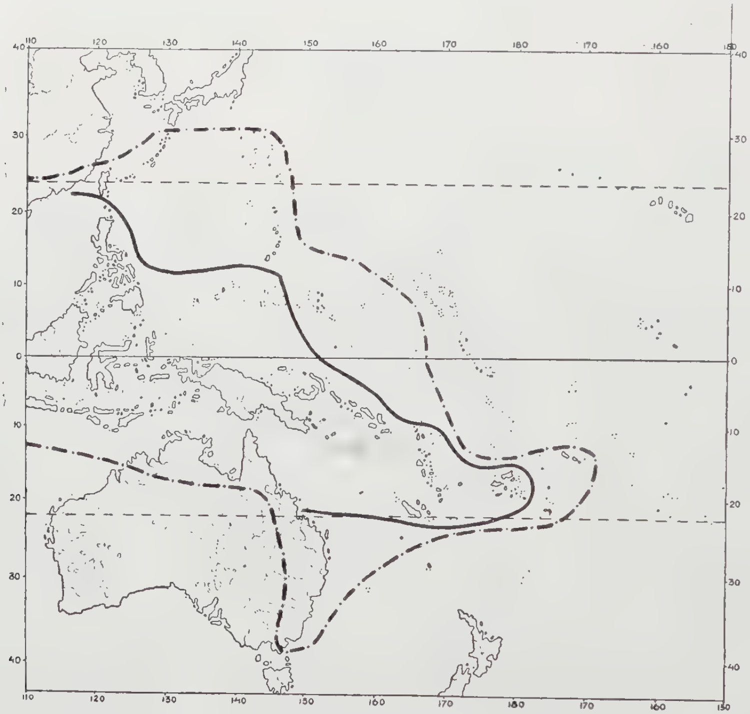

Fig. 1. Distribution in the Western Pacific Area of the Pteropinae (broken line) and of the Macroglossinae (heavy line).

In his "Herbarium Amboinense" Rumphius already described the dissemination by bats of some plants in the Moluccas. This was already mentioned by Ridley (1930, p. 349), but after comparing Rumphius' text I see that the names cited by Ridley will have to be changed as referring to: *Artocarpus champeden* (I: 109), *Annona reticulata* (I: 136), *Mangifera indica* and related wild species as *M. foetida, M. odorata* and *M. caesia* (I: 95).

Osburn (1865) described how some American bats transported seeds of *Brosimum alicastrum*, *Cordia collococca* and *Eugenia jambos* to their caves, and that one of them carried internally seeds of *Morus* (*Maclura*) *tinctoria*.

Ule (1900) drew the attention of botanists to the question in a short article in which he mentioned some American Moraceae as bat-dispersed. He referred to an unnamed publication by Fritz Müller, also cited without further indication in Ludwig's Lehrbuch der Biologie (1985), which apparently mentioned *Billbergia zebrina* and *B. speciosa* as dispersed by bats.

Huber (1910) went further and said that in the Amazonian forests of Brazil fruit bats are the most important of all agents of seed dispersal. This important ecological study seems to have been overlooked by most phytogeographists, though its remarks on bats have been quoted in Brehm's "Tierleben".

Huber mentioned some categories of fruits which seemed specially suited for this transport, in the first place the fleshy pods of some *Dalbergieae*, especially those of the genera *Dipteryx* and *Andira*. (The name Andira means bat in an Indian language and the Brazilian name of *Andira inermis* is "morceguiera"). Further he mentioned as bat-dispersed plants whose fruits are provided with large and hard kernels species of *Licania*, *Couepia*, *Parinarium*, *Saccoglottis*, *Vantanea* and *Poraquebia*. He gave detailed observations on this dispersal in the palm *Iriartea exorhiza*. An other important group is according to him formed by the *Sapotaceae* and *Annonaceae* with soft pericarp and relatively large seeds, which separate easily from the flesh. Finally he distinguished a group of fruits, with small seeds that pass the intestines of bats; they are found especially in *Moraceae* like *Cecropia*, *Ficus*, *Bagassa*, etc.

In his extensive handbook Ridley (1930) collected data from many sources, but from the authors mentioned above only Rumphius and Osburn were quoted. The data on *Anacardium* and *Psidium*, marked with his name in table I, refer to observations made in America, the other ones were collected in the Old World. He gave as his opinion (p. 347) that "bats are the most important seed dispersers of any mammals" and adds that they are very voracious and can fly long distances.

Ridley shows an aversion of classificatory terminology, but his comments help in the elucidation of class-characteristics. He draws the attention to a group of fruits that seem to offer no attraction to other mammals and to birds, viz. many hard-fleshed, green drupes. On page 392 he distinguishes (in *Eugenia*) bird-fruits (small, juicy, coloured, produced on low branches) and bat-fruits (large, greenish, provided with a firm pericarp). On page 435–436 a similar distinction is made in the genus *Ficus*, where cauliflorous species with large, dull-coloured fruits are regarded as bat-dispersed (outspoken in *F. polysyce* and *F. fistulosa*), whereas small, coloured figs point to bird-dispersal. Species like *F. benjamina* are suited for both birds and bats.

The data collected by Ridley are mentioned in table I under his name as it does not seem necessary to refer to the original sources. The names of the diverse authors mentioned in this chapter and in later ones can be recognised in column 3.

In his book on carpobiology Ulbrich (1928) occasionally mentions bats, viz. in the discussion of the many juicy, large-seeded fruits in the tropics (p. 79–84). He differentiates but poorly between the many tropical fruit eaters, but mentions (mostly as a surmise) on page 84–85 some fruits as bat-fruits, e.g. *Achras sapota*, *Chrysophyllum cainito*, *Lucuma nervosa*, *Pouteria cainito* and *Mammea americana*. He also tries to give a characterisation of this type of fruit, in which he mentions the presence of long fruit stalks which would protect the fruits against the attacks of animals that do not fly.

The present author published two studies (1935, 1936*a*) in which lists of bat-fruits from Java were given but wherein also a characteristization of the class was attempted. As both studies were published in Dutch in a semi-popular periodical, the contents are incorporated in the present paper together with some later finds.

Docters van Leeuwen (1935) gave an enumeration of the seeds found underneath the resting places of fruit-bats.

Misled by some confusion in my popular paper he erroneously cited some plants as being considered by me as proven chiropterochorous, viz. *Zalacca edulis*, *Ceiba pentandra*, *Sechium edule*, *Nephelium lappaceum*, *Phyllanthus emblica*, *Ph. acidus*, and *Garcinia mangostana*.

In his book on Krakatau (1936) this author gave many data on the dispersal of shore plants by bats.

The data from the latter four studies are comparable and refer to Javanese bats, mostly *Cynopterus* species.

Baker and Baker (1936) (B.a.B. in table I column 3) mentioned a number of fruits eaten by *Pteropus* on an island belonging to the New Hebrides.

Dr. H. Felten from the Senckenberg Institute in Frankfurt a.M. wrote me that he had regularly found remnants of fruits underneath the colonies of bats in caves in El Salvador. The fruits belonged to *Spondias purpurea* L. and *Ficus* species. The bat species concerned were *Phyllostomus discolor verrucosus* Elliot (*Spondias*), *Artibeus jamaicensis* Leach (*Spondias*) and *Artibeus lituratus palmarum* Allen and Chapman (*Ficus*).

In 1954 Eisentraut published an emended compilation by H. Jansen on the biology of the *Megachiroptera* (from the Old World). Being a zoölogist he is in the first place interested in the zoölogical aspect of the problem. He collects data from zoölogists and gives in the chapter on food-habits a list of the fruits eaten (p. 374–377). Data on *Microchiroptera* from America are naturally not included, but many data published by botanists on the activity of *Megachiroptera* (almost all those mentioned above) are also missing. The case of *Borassus* mentioned by Eisentraut, is not taken over in our table I, as the bat exercised here a merely dystrophic activity. The case of *Areca catechu* (improbable after my experience from Java) is left out as not present in the source mentioned by Eisentraut. I include his other data in so far as they have not been mentioned here before.

For the kind of bat and the country involved I refer to the original sources.

Mr. A. M. Greenhall, zoölogist of the Department of Agriculture in Trinidad, allowed me the use of the manuscript of a study about to he published (GREENHALL, 1956). This important paper gives details on ± 50 fruits eaten by the three principal fruit-bats of Trinidad and Tobago, viz. *Artibeus jamaicensis*, *Artibeus lituratus* and *Carollia perspicillata*.

Mr. Greenhall started from the zoölogical angle, investigating the food of the bats in all seasons, but he shows a clear understanding for the botanical side of the question. He mentions some fruits as greedily attacked, but too heavy to be carried off by the local bats, e.g. those of the *Mangifera*, *Annona*, *Mammea* and *Persea* species, and *Eugenia malaccensis*, all marked by his name in column 3 of table 1.

TABLE I

List of plants, described as being dispersed by bats

Name	Family	Author
Achras sapota	Sapotac.	Ule, Hub., Rid., v. d. P., Eis., Greenh.
Acrocomia sp.	Palmae	Allen
Actinophloeas angustifolius .	Palmae	D. v. L.
Adinandra sp.	Theac.	Rid.
Aglaia sp.	Meliac.	D. v. L.
Anacardium occidentalis . .	Anacard.	Rid.
Anacardium rhinocarpus .	Anacard.	Pietri
Anamomis umbellulifera . .	Myrtac.	Greenh.
Andira inermis	Legumin.	Hub., Greenh.
Annona muricata	Annonac.	Hub., D. v. L., Eis., v. d. P., Greenh.
,, reticulata	,,	Rumph.
,, squamosa	,,	Greenh.
Anthocephalus cadamba . .	Rubiac.	Rid.
? Antidesma bunius	Euphorbiac.	D. v. L.
Areca glandiformis	Palmae	Rumph.
Arenga pinnata	,,	D. v. L.
Artocarpus communis (incisa)	Morac.	D. v. L., Rid., B. a. B., Rumph., Eis.
,, elastica.	,,	D. v. L.
,, champeden . .	,,	Rumph.
,, integra	,,	D. v. L.
Attalea sp.	Palmae	Rid.
Azadirachta indica.	Meliac.	Eis., Hall
Baccaurea racemosa	Euphorb.	D. v. L.
Bactris speciosa	Palmae	D. v. L., v. d. P., Greenh.
Bagassa sp.	Morac.	Hub.
Bassia latifolia	Sapotac.	Rid.
Billbergia speciosa	Bromeliac.	Müller
,, zebrina	,,	Müller
Brosimum alicastrum . . .	Morac.	Osb.
Bouea macrophylla	Anacard.	v. d. P.
Byrsonima spicata	Malpighiac.	Greenh.
Calocarpum mammosum . .	Sapotac.	Greenh.
Calophyllum inophyllum .	Guttifer.	Rid., D. v. L., v. d. P.
,, pulcherrimum	,,	Rid.
? Canarium commune . . .	Burserac.	D. v. L., v. d. P.

Name	Family	Author
Carica papaya	Caricac.	Rid., D. v. L., v. d. P., B. a. B., Greenh., Eis.
Caryota rumphiana	Palmae	D. v. L.
Cecropia sp. (incl. peltata) .	Morac.	Ule, Hub., Greenh.
Ceratonia siliqua	Legumin	Ulbr.
? Cereus hexagonus	Cactac.	Greenh.
Chrysalidocarpus sp.	Palmae	v. d. P.
Chrysophyllum cainito . . .	Sapotac.	Greenh.
Chrysobalanus icaco	Chrysobal.	Greenh.
? Citrus sp.	Rutac.	Eis.
? Clibadium surinamense .	Compos.	D. v. L.
? Coffea sp.	Rubiac.	Greenh., Pietri
Coccoloba uvifera	Polygonac.	Greenh.
Cordia bicolor	Borragin.	Greenh.
,, colloccocca	,,	Osb., Greenh.
,, abyssinica	,,	Eis.
Corypha utan	Palmae	D. v. L.
Couepia sp.	Chrysobal.	Hub.
Coussapoa sp.	Morac.	Ule
Curtisia faginea	Cornac.	Rid.
Cycas rumphii	Cycadac.	D. v. L.
Cynometra cauliflora . . .	Legumin	D. v. L., v. d. P.
Cyrtandra sulcata	Gesner	D. v. L.
Diospyros mabola	Ebenac.	Greenh.
,, melanoxylon . .	,,	Rid.
,, embryopteris . .	,,	Rid.
Dipteryx spp.	Legumin.	Hub.
,, odorata	,,	Greenh.
Dracontomelum mangiferum	Anacard.	B. a. B.
? Durio zibethinus	Bombac.	D. v. L.
Dysoxylum sp.	Meliac.	D. v. L.
Elaeocarpus parvifolius . .	Elaeoc.	Rid.
? Elaeocarpus ganitrus . . .	,,	v. d. P., Eis.
? Epiphyllum hookeri . . .	Cactac.	Greenh.
Eriobotrya japonica	Rosac.	Rid., Eis.
Eugenia aquea	Myrtac.	D. v. L.
,, cumini	,,	Eis.
,, densiflora	,,	v. d. P.
,, grandis	,,	Rid.
,, javanica	,,	Rid., v. d. P.
,, jambolana	,,	Rid.
,, jambos	,,	Osb., Eis., Greenh.
,, polyantha	,,	D. v. L., v. d. P.
,, malaccensis	,,	D. v. L., v. d. P., Eis., Greenh.
,, striata	,,	v. d. P.
Evodea sp.	Rutac.	D. v. L.
Fagraea (Cyrtophyllum) sp.	Loganiac.	D. v. L.
,, peregrinum . . .	,,	Rid.
,, fragrans	,,	Rid., D. v. L., Corner.
? Ficus ampelas	Morac.	D. v. L.
Ficus benjamina	,,	Rid., D. v. L., Greenh.
,, bengalensis	,,	Rid.
,, copiosa	,,	B. a. B.
,, elastica	,,	D. v. L.
,, callosa	,,	D. v. L.
,, fistulosa	,,	D. v. L., v. d. P.
,, fulva	,,	D. v. L.
,, glomerata	,,	Rid., D. v. L., v. d. P.

Name	Family	Author
,, hispida	,,	D. v. L.
,, religiosa	,,	Rid.
,, ribes	,,	D. v. L., v. d. P.
,, polysyce	,,	Rid.
,, retusa	,,	D. v. L.
,, umbellata	,,	Baker
,, variegata	,,	D. v. L., v. d. P.
,, sycomorus	,,	Eis.
? Flacourtia rukam	Flacourt.	D. v. L.
? ,, indica	,,	Greenh.
Freycinetia sp.	Pandan.	Baumann
Glochidion ramiflorum	Euphorb.	B. a. B.
Gluta renghas	Anacard.	D. v. L.
Guettarda speciosa	Rubiac.	D. v. L.
Hernandia peltata	Hernand.	D. v. L., v. d. P.
Hippomane mancinella	Euphorb.	Lasser
Hyphaene thebaica	Palmae	Eis.
? Hylocereus lemairii	Cactac.	Greenh.
Inocarpus edulis	Legumin.	Rid., D. v. L.
Iriartea exorhiza	Palmae	Hub.
Irvingia barteri	Simarub.	Eis.
Lansium domesticum	Meliac.	D. v. L., Eis., v. d. P.
Licania sp.	Chrysobal.	Hub.
Litsea polyantha	Laurac.	D. v. L.
Livistona australis	Palmae	Rid.
? Livistona rotundifolia	,,	D. v. L., v. d. P.
Livistona chinensis	,,	Rid.
Malphighia glabra	Malpighiac.	Greenh.
Mammea americana	Guttif.	Greenh.
Mangifera indica	Anacard.	Rid., D. v. L., v. d. P., Greenh., Eis.
,, foetida	,,	Rumph.
,, odorata	,,	Rumph.
Maniltoa gemmipara	Legumin.	D. v. L.
? Melastoma malabathricum	Melastom.	D. v. L.
Melia azedarach	Meliac.	Rid., D. v. L.
Melicocca bijuga	Sapindac.	Greenh.
Mimusops elengi	Sapotac.	v. d. P., Greenh.
,, (Manilkara) bidentata	,,	Greenh.
Morinda citrifolia	Rubiac.	D. v. L.
Morus (Maclura) sp.	Morac.	Eis.
,, (Chlorophora) tinctoria	,,	Osb., Greenh.
? Morus nigra	,,	Eis.
? Muntingia calabura	Elaeocarp.	D. v. L.
Musa spp. div.	Musac.	Rid., D. v. L., v. d. P., Greenh., Eis.
Nauclea elegans	Rubiac.	? Rumph.
Nephelium spp.	Sapindac.	Rid.
,, lappaceum	,,	D. v. L.
Ochrocarpus congregatus	Guttif.	D. v. L.
Olea laurifolia	Oleac.	Rid.
Oncosperma filamentosa	Palmae	D. v. L.
Oreodoxa oleracea	,,	Greenh.
Palaquium gutta	Sapotac.	Rid., v. d. P.
Pandanus tectorius	Pandanac.	Rid., D. v. L.
,, odoratissimus	,,	Eis.
Parinarium sp.	Chrysobal.	Hub.

Name	Family	Author
? Passiflora foetida	Passiflor.	D. v. L.
Passiflora quadrangularis	,,	Greenh.
Persea gratissima	Laurac.	Eis., Greenh.
Phoenix dactylifera	Palmae	Rid.
Pimenta racemosa	Myrtac.	Greenh.
Piper aduncum	Piperac.	D. v. L., v. d. P.
,, retrofactum	,,	D. v. L.
Pipturus incanus	Urticac.	D. v. L.
Polyalthia sp.	Annonac.	Rid.
,, longifolia	,,	Eis.
Poraquebia sp.	Icacinac.	Hub.
Pouteria multiflora	Sapotac.	Greenh.
Prunus persica	Rosac.	Eis.
Psidium guajava	Myrtac.	Rid., D. v. L., v. d. P., Greenh., Eis., B. a. B.
Putranjiva roxburghii	Euphorb.	Greenh.
Saccoglottis sp.	Humiriac.	Hub.
Sandoricum koetjape	Meliac.	D. v. L.
Sapindus rarak	Sapindac.	D. v. L., Greenh.
Sideroxylon sundaicum	Sapotac.	Rid.
,, quadriloculare	,,	Greenh.
Sonneratia caseolaris	Sonneratiac.	v. d. P.
Spondias dulcis (cytherea)	Anacard.	D. v. L., Rid., Eis., Greenh.
,, lutea	,,	D. v. L.
,, purpurea (mombin)	,,	Felten, Greenh.
Strychnos nux vomica	Loganiac.	Eis.
Symplocos sp.	Symploc.	Rid.
Terminalia catappa	Combretac.	Rid., D. v. L., v. d. P., Greenh., Eis., B. a. B.
Thevetia neriifolia	Apocynac.	v. d. P.
Vantanea sp.	Humiriac.	Hub.
Xerospermum sp.	Sapindac.	Rid.
Zizyphus sp.	Rhammac.	Rid.

I included these data in the list because the plants concerned had already been mentioned as dispersed by other, larger fruit-bats and because the observations in America confirm the universal preference of bats for these fruits.

Though there was no effort to distinguish between true bat-fruits and those that are incidentally eaten by bats, Mr. Greenhall noted that in the three *Cactaceae* mentioned (*Cereus*, *Epiphyllum*, *Hylocereus*) the bats did for some reason or other not contribute to the dispersal. I marked these names (and *Coffea*) in table 1 with a question mark, as I fear an incidental "derailment" of the bats here towards these purple bird-fruits.

The families that dominate in the list are resp. the *Moraceae*, *Palmae*, *Anacardiaceae*, *Sapotaceae* and *Meliaceae*, but chiropterochory has—apparently independently—developed in many other families.

A list like table I will always remain to some extent unsafe. It may include data given by zoölogists who tend to pay more attention to the plants as providing nutrition to bats than to the actual dispersal of seeds (cf. *Borassus* on p. 294). When I saw a *Cynopterus* bite off pieces of the fruits of *Sechium edule* without dispersing the seeds I did of course not include this species in the list.

Of course not all the items of the list have the same biological importance. A complete investigation should also consider the negative side, viz. the degree to which other dispersers are excluded; this point is discussed in chapter C.

I put a question mark before some names of doubtful importance. Some data evidently refer to incidental and abnormal visits due to special circumstances, as bats in a hunger period, the presence of cultivated temperate fruits in tropical mountains (cf. the introduction to chapter C).

A drawback of the list, obscuring the importance of bat-dispersal of wild fruits in natural vegetations, is that most observers paid excessive attention to plants cultivated in gardens. The fruits of the genus *Citrus*, for instance, though mentioned in some isolated instances, are quite atypical, and are in some other studies especially mentioned as being refused by bats.

Greenhall (1956) who included many Asiatic plants grown in gardens, also made remarks in this direction. He expects that many cases could be uncovered in the forest, like the discovered one of the high balata trees (*Mimusops* or *Manilkara*) in the virginal forests of Trinidad. His (and Pietri's) find of *Coffea* seeds underneath roosts and in caves is clearly a derailment of the bat—for these fruits are neither in Africa nor in Asia, dispersed by bats.

In some cases from Docters van Leeuwen (1935) I fear contamination with bird droppings as the fruits in question, often borne on low plants are unfit for bats and are mostly ornithochorous. This refers to *Passiflora*, *Clibadium*, *Melastoma*, *Antidesma* and probably to *Flacourtia*. In a former study, on seeds dropped by the bird *Aplonis panayensis* underneath its nest, this author mentioned seeds of the above *Clibadium* and *Melastoma* species. The case of *Durio zibethinus* is enigmatic, as this fruit can obviously be handled only by very large mammals. The finds of kernels of *Canarium* gnawed off by bats in Java are incidental. In the home country of the plant the seeds are spread by fruit-pigeons. For parallel cases of ornithochorous fruits eaten by bats I refer to *Muntingia calabura* (cf. p. 304), *Livistona rotundifolia* and *Elaeocarpus ganitrus* (cf. p. 301).

C. Characteristics of bat fruits

Of course fruit-bats eat whatever they can find and like, irrespective of the question whether the food is endemic in their habitat or not, and whether their activity is required for maintaining the natural composition of the vegetation by seed dispersal. In inhabited regions with many cultivated plants this will be very obvious (cf. *Livistona* and *Elaeocarpus* on p. 301). In Java they chew soft, new leaves of *Sechium edule*, in Trinidad those of *Ficus religiosa*,—a purely dystrophic activity. In the rare cases that nectar is taken from intact flowers or that parts of flowers and inflorescences are eaten, there may occur pollination. Sometimes whole flowers are squashed. Dystrophic activity of the latter kind was rarely found in Java (*Parkia*, *Durio zeylanicus* in the Botanical Garden), but occurs on a larger scale in Eastern

Indonesia and especially in the border regions in Australia (c.f. RATCLIFFE, 1931). Destruction of seeds is also rare (cf. *Calophyllum*, *Sechium* and *Borassus* on p. 298, 303 and p. 297). On the whole, fruit "destined" for bats seem to possess an efficient protection for their seeds. In a region like sub-tropical Australia, where many foreign fruits are cultivated and where *Pteropus* is met with as a migrator, the connection between bats and fruits will be more or less incidental. There too we find, nevertheless, a preference for native and introduced bat fruits, with mangoes and custard-apples at the top of the food list and with pome-fruits and especially *Citrus* at the bottom (cf. RATCLIFFE, 1931).

We have to recognise that bonds with bats may be a secundary deviation from more ancient bonds with birds and that the boundary line between the two classes may be unsharp.

All this, however, should not prevent us from looking in tropical fruits for features, which might bring them into the special sphere of interest of the fruit-eating bats. The stamp of the bat! As the fruit is a part with an outspoken ecological function it seems plausible to assume that local ecological factors (in casu the dispersing animals) may have had a profound influence on the evolution of its characteristics. We may leave aside the question whether this was a purely selective influence but, though we have no clear understanding of the way the influence may have acted, it seems unsatisfactory to assume that a special type of fruit would develop incidentally and without regard to the presence of agents fit to disperse such a fruit. A taxonomous group with fruits mainly fit for dispersal by bats would certainly be handicapped in a region without fruit-bats.

Of course when a general picture has been developed of the characteristic features of an ecological class, it will always be possible to discover cases where one of the features is missing. This is just as in the classes of floral biology, to whose acceptance only negativists object on the futile ground that there are transitional and non-classifiable forms. In this connection I would draw the attention to a quotation from Whewell in Arber's "Natural Philosophy of Plant Form" (p. 67): "A natural class of objects is determined, not by a boundary line without, but by a central point within; not by what it strictly excludes, but by what it eminently includes".

After some tropical ecological experience it is quite well possible to recognize a typical bat fruit, even if it were only because transport by other agents appears to be excluded.

A second step in the research is the recognition of the sociological importance of the bonds in the natural community.

A short characterisation of the class was given in my discussion of the ecological classification of leguminous fruits (1956*a*). It is as follows:

1) Edible part soft or hard, 2) dimensions of fruit and seed large, up till those of a manggo, 3) dull colour, 4) unfresh odour, 5) attached to the tree till after maturity, 6) tough skin (indehiscence) possible, 7) exposure outside the foliage.

For a full discussion I will follow my study of 1935.

For a comparison with the class of bat-flowers, which shows parallel adaptations, I refer to my monograph on this subject (1936*b*).

1. *Colour*

It has many times been mentioned that the typical bat-fruit is visually not conspicuous, being greenish or brownish.

I may refer here to the green drupes and figs mentioned by Ridley (cf. p. 293) and to Fritz Müller (cf. p. 293) who was struck by the fact that the fruits of the chiropterochorous *Billbergia* species are dull coloured in contrast to those of the mostly gaudy ornithochorous relatives.

In chapter E this point will be stressed for tropical table fruits and in chapter D 2 for a number of sea-shore fruits. It will be confirmed by a perusal of the tables I and II, especially when the incidentally bat-dispersed fruits, discussed on p. 299 are left out of consideration. The pigeon plum *Eleaocarpus ganitrus* (a bird fruit) and *Livistona rotundifolia* have blue fruits, which are rather small and without smell. The fruits of both species are nevertheless eagerly sought after by bats in Java, where the trees have been introduced into gardens. This transition is facilitated by the open structure of their crowns—so favourable to bats.

For a colourblind bat the absence of colour is no handicap, but it may be so for birds. Sometimes a lighter shade of colour may offer some help to bats in the night.

2. *Odour*

Fruit bats have a keen sense of smell as already indicated by the structure of the nasal cavity. No wonder therefore that the presence of a distinct odour is a character of the chiropterochorous fruits, which differentiates them from the ornithochorous ones.

There is even a slight differential characteristic in this respect with fruits eaten by other mammals, arboreal as well as terrestrial ones. Bats have a taste which differs from the one of other mammals, who, like man, seem to prefer, a fresh "fruit odour". Fruit-bats themselves often spread an unfresh, rancid or musty odour often emanating from special glands and seem to like fruits with a similar smell, often reminding of fermentation. Nectarivorous bats have a preference for flowers emitting a similar odour (cf. van der Pijl, 1936*b*).

One day we may be able to define this characteristic in chemical terms. The very rancid fruits of *Morinda citrifolia* might be analysed in order to find out whether they contain butyric acids or related substances. At an earlier occasion I mentioned that the fruits of the cauliflorous *Ceratonia siliqua*, sought after by the Egyptian bat *Cynonycteris Geoffroyi* (according to Ulbrich (1928)), were actually found to contain butyric acid. The comparison with mouse urin, so often made in regard to the odour of bat flowers and bat fruits, also suggests a chemical investigation in this direction.

In the genus *Ficus* it is remarkable that large, dull coloured, and stem-borne figs, spread an odour of fermentation.

The smell of wild manggoes is notorious. For table fruits see chapter E.

As in bat flowers the typical smell arises after sunset, I tried to find out whether there is a similar rhytm in the odour production in a typical bat fruit, viz. that of *Psidium guajava*. No indication of this was found. The odour persisted for some days, also during daytime. Corner (1940, p. 111) cited an opinion that the fruits of a *Mangifera* species ripen during the night.

3. *The dimensions of the fruits*

Generally speaking, a large size may also be a differential characteristic. It gives sense to the often mentioned fact that there are in the tropics so many large, juicy fruits with large seeds.

Bat fruits may be just some cm large, but also so large, that they cannot be swallowed or transported by birds. Some large fruits are also fit for bird food because they can easily be picked into pieces, as those of *Carica papaya*, liked by many animals. Typical bat fruits are not so readily broken up into smaller parts. Large birds like hornbills, some pigeons, crows and cassowaries (cf. p. 310) remain in this respect not so far behind bats, (with nutmegs, *Canarium* and palms), but the fruits of *Mangifera* (100–200 gr) and others are too large for them. Bats even can tear off pieces from the gigantic compound fruits of *Artocarpus* species.

The possible large dimensions have a relation to the way of transport, which is rarely endozoic, but usually synzoic. The fruits are (as many observers since Huber have reported) transported in the mouth to a quiet spot, sometimes hundreds of meters off. Osburn found half a mile and Greenhall some hundreds of yards. This spot may be the roosting place, but it is not necessarily so, certainly not in the case of *Pteropus*. In forests one often finds heaps of fresh débris under branches where no bats are sleeping. In Javanese crater regions heaps of *Eugenia striata* seeds are common. Greenhall distinguished in America too such fixed "digesting places" from the roosts.

In the case of cave dwellers transport of the fruits to the caves would be fatal to the seeds and what is actually found in the caves may be the remnants of only the last meal, taken home.

This kind of behaviour on the other hand makes that the distance of dispersal is less impressive than one might be inclined to deduce from the tens of kilometers *Pteropus* can fly. For small seeds the situation is different as we shall see.

The accumulation of many seeds on one spot in the forest, later on to be recognised by dense groups of seedlings, is another drawback.

Undoubtedly there is in the dimensions of the fruits some differentiation between those suitable for the large *Megachiroptera* like *Pteropus* and those for the smaller ones, for instance of the genus *Cynopterus*. *Pteropus* may carry fruits weighing up to ± 200 g, whereas *Cynopterus* as an average is fully loaded with a fruit of *Psidium* or of *Achras sapota* of 75 g. I observed that *Cynopterus* had to gnaw the large fruits of a manggo on the tree. *Pteropus*, however, takes small figs too.

I already cited from Greenhall (1957) that the three Trinidad fruit-eating *Microchiroptera* were unable to transport some recognised bat-fruits as a whole or in parts, as these fruits were too large for them. Some other fruits (e.g. those of *Terminalia catappa*) could be carried off only by the larger local bats (the *Artibeus* species).

4. *Size of seeds and kernels*

This runs parallel with that of the fruits, but is sometimes decisive, viz. in smallish fruits, as is to be seen in Ulbrich (1927) Figs. 13 and 16, where a number of bat fruits are figured with the strikingly large seeds that are left behind after the meal.

In the centre of Javanese cities one may find heaps of bat's debris under the protruding part of a roof. Systematic collecting of such remains in tropical botanical gardens would yield useful results. The writer would gladly receive reports of seeds found.

It has been related by many observers (cf. Ratcliffe (1931), van der Pijl (1935), Baker and Baker (1936), and Greenhall (1956) that neither *Megachiroptera* nor *Microchiroptera* swallow the substance of the fruits as such. Sometimes the pericarp is gnawed off separately, sometimes (with smaller seeds) the flesh and the seeds are squashed and pressed out together, but always the solid matter is ejected as dry pellets. Only the juice is swallowed. In the stomach one finds no solid substance but only a jelly. The excreta, which I collected for years, contain as a rule no seeds. The gullet is narrow and the intestine remarkably short.

Eisentraut (1945) already remarked that this way of feeding on vegetable matter is most fitting to the organization of a bat. A large abdomen such as would be required for the digestion of material full of cellulose might impair its power of flight.

It does not seem to be strictly necessary for the seeds that are gnawed off, to be protected by a very hard coat—another difference with the endozoic bird fruits. Some disagreeable property of the seed seems sufficient to prevent damage. In many *Sapotaceae* and *Annonaceae* we see that the seeds are so slippery that they escape as soon as the transported fruit is attacked.

The opinion that *Pteropus* sometimes also chews and eats the seeds themselves (e.g. those of *Calophyllum inophyllum*) has been recorded, though with some doubt, by Eisentraut (1945). In my observations of this plant I never saw anything of the kind.

Perhaps the situation is different with some transitional fruit eaters among the American *Microchiroptera*. Ridley cites old reports in which it is said that seeds and insects were found together in the stomach of *Vampyrus spectrum*. The available data about such American tropical bats are very unsatisfactory. Recently Felten (1956) reported that even *Glossophaga soricina leachii* (Gray), which is known as a flower visitor, prefers during the rainy season insects and soft fruit flesh to nectar.

The large size of the seeds is especially striking in the group of more or less certainly chiropterochorous *Leguminosae* which I discussed in a previous article (1956)*a*. They are often cauliflorous and have usually one-seeded, drupe-like pods. The fruits of one of them (*Cordyla*) are said to possess the typical colour and smell as of *Mangifera* fruits; in others representing this group colour and position of the fruits are typical for bat fruits, but more details are wanted. The group includes *Cordyla pinnata*, *Swartzia fistulosa*, *Cynometra cauliflora*, *Inocarpus edulis*, *Detarium senegalense*, *Angylocalyx* spp., *Andira inermis*, *Maniltoa gemmipara*, *Dipteryx odorata*.

I said that the excreta contain as a rule no seeds.

An exception should be made for some very small, smooth seeds, which were found to be swallowed accidentally. I already cited some cases from Huber and Osburn (*Maclura*, *Cecropia*, *Ficus*, *Bagassa*). In Java I found in the excreta seeds of *Piper aduncum* of which the green catkins acquire just before ripeness the consistency of a sweet jelly. Several kinds of animals eat them. At night they are plucked by bats and transported, after which the bats strip the sweet layer with the small seeds from the axis, squash this mass and leave the dry press cakes on the axis tip. Many seeds are swallowed and may later be found in the excreta, which are often spurt against walls when the bats alight on gutters. The same happens with the seeds of the introduced garden tree *Muntingia calabura*, which is ornithochorous, but readily accepted by bats. DOCTERS VAN LEEUWEN (1936) found seeds of *Cyrtandra sulcata* in excreta. GREENHALL (1957) found that *Artibeus lituratus* swallowed part of the seeds of *Psidium*.

The genus *Ficus* takes a somewhat intermediary position. After feedings on *Ficus* fruits *Pteropus* and *Cynopterus* were usually found to have no "seeds" in the intestines. Others reported the same find from India and Africa. From time to time, however, Docters van Leeuwen and I found some seeds in *Pteropus* and *Cynopterus*, a.o. of *F. fistulosa* and of *F. glomerata*. These exceptions may be ecologically important for transport over greater distances, though the evacuation is probably very fast. *F. fistulosa* was found in Krakatau as early as 1905. The presence of *Ficus* in clefts of walls therefore may not always be due to birds.

Sometimes the chewed pulp with small seeds is thrown as a sticky lump against trees and walls.

Prof. H. G. Baker wrote me that the walls of the Botany Department in Achimota (Gold Coast) become in this way streaked with the expectorates of the bats *Epomophorus gambianus* and *Nanonycteris veldkampii*. They contain many seeds of *Ficus umbellata*.

5. *Consistency and morphology of the edible parts*

Bats like a soft, sweet fruit flesh as that of many *Sapotaceae*, *Annonaceae* and *Moraceae*. They accept, however, also hard and sour flesh, present in a thin layer—as in the fruits of wild *Eugenia* and *Elaeocarpus* species, *Averrhoa*, *Phyllanthus*, many palms and especially in the many diplochorous fruits found near the seashore, which are discussed in chapter D.

An unedible tough peel, which does not dehisce, is no obstacle, as it is torn off (c.f. *Lansium*, *Baccaurea*, *Nephelium* and *Artocarpus*). This point again is somewhat a differential characteristic with bird fruits, which when large and tough are dehiscent, so that the interior becomes accessible. This happens especially in fruits of "low standing", where the pericarp is protective only and the sarcotesta or aril edible.

In my study on the hierarchy of edible layers in fruits (1956*a*) I composed a scala of what in this respect is to be regarded as primitive and progressive. The range is: A. the nude, edible sarcotesta, B. the covered sarcotesta, C. the arillode (partial sarcotesta), E. the aril, F2. the endocarp pulpa, F3, the mesocarp.

My impression is that bird fruits dominate in the phases A and B, but that many fruits in phase B already became chiropterochorous, as illustrated by *Baccaurea*, *Lansium* and many *Sapindaceae*. It is even possible, that *Cycas rumphii* in phase A is truly chiropterochorous, though Gymnosperms as a rule rely on other animals. *Musa* is a good instance of phase F2.

In the *Leguminosae* (c.f. my study of 1956*a*) there is certainly a priority of ornithochory in phase B, though probably *Inga* in this phase already developed indehiscent, chiropterochorous pods. *Parkia* did this in phase F2.

Most chiropterochorous fruits (also in the *Leguminosae*) are in phase F3.

6. *Position of the fruits on the tree*

Bat fruits and bird fruits have one feature in common, by which they differ from fruits spread by ground mammals, viz. that the mature fruits remain attached to the tree.

In one other respect there is, however, a strong contrast between the two former classes, viz. that bat-fruits occupy a peculiar position on the tree, one that enables the bats to fly to them without inconvenience from the foliage.

This position may be:

a) on the surface of the crown, at the ends of the twigs (as in *Achras*, *Psidium*).

b) on pendulous branches or peduncles; in this case the fruits dangle in open spaces in or underneath the crown. This "flagelliflory" or "penduliflory" can be seen in all degrees of development in *Melia*, *Mangifera*, *Musa*, *Spondias*, *Morinda*, etc.,

c) on the old branches of an open crown, or on the trunk (cauliflory), (Sometimes b) and c) are combined, as in many *Ficus* species, *Lansium*, *Baccaurea*, *Phyllanthus* and many palms),

d) in pagoda-shaped trees, as is very striking in *Terminalia catappa*. In a general discussion of the construction of the crown of many tropical trees Bremekamp (1936) described the curious construction of this tree and others with the foliage in tiers. For a special reason I refer also to the analysis of Corner (1940), who coined the terms "pagoda-tree" and "Terminalia-branching".

The two phenomena were there described for Malaya as occurring in: *Alstonia*, *Ochrosia*, *Terminalia*, *Endospermum*, *Salmalia*, *Achras*, *Palaquium*, *Manilkara*, *Sterculia*, *Archytaea* and *Elaeocarpus*. I might add *Ceiba* as an introduced tree.

To find an ecological interpretation of the latter construction I beg to compare this enumeration with our tables I and II, wherein we find the names of *Ochrosia*, *Terminalia*, *Achras*, *Palaquium*, *Manilkara* and *Elaeocarpus*.

Of *Salmalia* (*Bombax Valetonii*) and *Ceiba* I have already reported (1936) that they are pollinated by bats.

Of the 12 genera only *Alstonia*, *Endospermum*, *Archytaea* and probably *Sterculia* have no intimate connections with bats.

In Corner's book (1940)—a goldmine for ecological details—the crowns of some other trees are especially described because of their curious, open structure. One is *Duabanga sonneratioides* Buch.-Ham. (*D. grandiflora* Walp.), which is certainly chiropterophilous (c.f. Corner's data on the flowers of this species and my own (1956*b*) on those of *D. moluccana*). The others belong to the genus *Fagraea*. *F. crenulata* has the pure pagoda-shape (c.f. his plate 121), and *F. fragrans* has this structure combined with flagelliflory, the tops of the branches being pendulous—as in *Duabanga*. In this genus we find pronounced chiropterochory—as described by Corner himself for *F. fragrans*.

I shall not discuss here, whether form or function is primary in this respect but the typical position is sometimes an easy criterium to decide from a description or from a figure whether a plant might be chiropterophilous or chiropterochorous. The stamp of the bat even on the vegetative system!

In many species the special position of the flowers, and consequently of the fruits, is important for both pollination and seed dispersal, so that they are in two ways bat plants. I mean some *Sapotaceae* like *Bassia latifolia* and probably some *Palaquium* and *Madhuca* (*Payena*) species, further to *Musa* spp., *Sonneratia caseolaris*, *Eugenia cauliflora*, *Freycinetia insignis* and perhaps *Kigelia*, *Adansonia*, *Parmentiera*, *Duabanga* and *Parkia* species.

The rise of bat flowers in a group can sometimes been seen as following an earlier development of chiropterochory.

Let us add some remarks on flagelliflory and cauliflory.

The significance and the actual importance of these positions in relation to the physiology of *Megachiroptera* has been fully discussed by me in previous articles (1936, 1941, 1956*a*). These papers dealt principally with the parallel case of pollination by bats, but fruits were sometimes used for comparison. Flagelliflory and cauliflory, considered by many earlier writers from many angles as peculiarities of the tropics, were recognised by me as mostly adaptations to the visits of bats. The almost complete absence of the two phenomena in Europe often considered as normal is the peculiarity,—to be explained by the lack of *Megachiroptera*.

Ulbrich (1928) was the only one who had somewhat the correct, though vague, understanding in regard to cauliflorous fruits, as quoted before. On p. 93 he also cited incidentally, without expressing its significance in this connection, the dispersal by bats of *Ceratonia siliqua*, the typical "European" cauliflorous plant. This date regards Egypt, in the curious Northern offshoot of the area of distribution of the *Megachiroptera*, which terminates in Cyprus.

Although I admit anew that cauliflory may sometimes be ecologically meaningless, I maintain that it is mostly ecologically important. This sometimes concerns the pollination of the flowers but mostly the dispersal of the seeds, the feature which interests us here.

For the other cauliflorous *Leguminosae* (cf. the chiropterochorous group mentioned on p. 304) this connection has already been demonstrated in my special study (1956*a*). A strikingly large part of the group shows cauliflory (*Cordyla*, *Swartvia*, *Cynometra*, *Angylocalyx*). Further it is very rare in the family.

Among the plants mentioned in table I cauliflory is found in species of *Ficus*, *Annona*, *Lansium*, *Baccaurea*, *Eugenia*, *Artocarpus*, etc. In the palms the cauliflorous position of the flowerstands, due to the organization type of the family, in combination with the pendulous stalks (flagelliflory), brings the fruits into a favourable position underneath the crown.

For many other cauliflorous, juicy fruits the actual bat-dispersal remains to be proven. Especially observations in tropical America should fill the gaps in our knowledge. I remind of the several cauliflorous, edible melastomataceous, sapotaceous and myrtaceaus fruits occuring in America. Think of *Marlieria edulis* and *Myrciaria* discussed and figured together with the African *Anacardiacea Trichoscypha ferruginea* in ULBRICH (1928) (Fig. 16). This author already remarked (p. 82) that it is striking how markedly species with juicy fruits dominate amongst cauliflorous trees. To prove this, he analysed the list of African cauliflorous species given by MILDBRAED (1922).

A list of all known cauliflorous plants, stating the accompanying characters of their fruits, was prepared by me before the war. It was lost, but would anyhow have taken too much space here.

In some cases of cauliflory a bond with a special way of pollination is clearly excluded, so that the special position can be of importance only in connection with the fruits. *Artocarpus integra* bears its male inflorescences in the crown near the tips of branchlets, whereas the female inflorescences are found near the base of the larger branches or on the trunk. In *Stelechocarpus burahol*, with certainly chiropterochorous, large, juicy, large-seeded and greyish fruits, the arrangement is the same.

D. BAT-DISPERSAL IN SPECIAL AREAS

1. *General remarks*

It may prove important, to study not only the general significance of bat-dispersal, but also its quantitative influence in special vegetations.

The usual "biological spectrum" covers the diverse "life forms" and may serve to characterize temperate and arid floras in their relation with the climatic periodicity in their region. We are, however, still badly in need of other biological spectra, which could express the relation with factors, climatic as well as biotic, which are of importance for the reproduction of the plants. A pollination spectrum and a dissemination spectrum would doubtless help us to obtain a better understanding of tropical floras.

Bat-dispersal might then prove to be of unequal importance in diverse tropical and subtropical vegetations. The first phases in the succession, when trees are as yet absent, are, of course, unable to harbour fruit-bats.

Most of the species enumerated in table I belong to open vegetations in sub-optimal condition, to sub-climaxes, secundary forests and the like, in tropical and adjacent subtropical regions. The trees mentioned have mostly a maximum-height of 25 m. The impression created by the table may be somewhat onesided owing to an as yet unsufficient analysis of the rain forest proper. However, many of the trees from earlier stages in the succession will persist in the lower stories of the forest. Many of the moraceous, meliaceous and sapotaceous trees from the higher stories may also be bat-dispersed (cf. Huber's remarks on p. 293 and those of Greenhall on *Manilkara*, on p. 299). Fruit bats do live in the rain forest up till high altitudes.

We are not yet in a position to extend these considerations very far, and will have to limit ourselves to some special cases.

2. *Diplochory on pacific shores*

Chiropterochores are especially abundant in the vegetation near the sea. The principal species from the Western Pacific have been collected in table II. The chiropterochory of most of them is a well-established fact, but of some it is, though probable, not yet proven.

TABLE II

Calophyllum inophyllum
Cerbera manghas
Cordia subcordata
Cycas rumphii
Guettarda speciosa
Hernandia peltata
Inocarpus edulis
Morinda citrifolia
Ochrosia parviflora
Pandanus spp.
Sonneratia spp.
Spondias lutea
Terminalia catappa
Ximenia americana

From American shores I could add many species from the "tropical littoral woodland" as *Coccoloba uvifera*, *Chrysobalanus icaco* and *Hippomane mancinella*. As Dr. Tobias Lasser from Caracas wrote me, the latter is spread on the Venezuelan beach by microchiropterous fruit bats. Ridley mentioned the apple-like, greenish yellow fruits as typical drift-fruits that are also eaten by goats and tortoises.

Phoenix paludosa from Malayan coastal swamps is probably another asiatic case of dispersal by both sea and bats. If this is true it would be ecologically intermediate between the majority of palm fruits and those of *Nipa* and *Cocos*, which are entirely sea-dispersed.

Perhaps the presence of so many chiropterochores near the Pacific shore explains the fact that *Pteropus* species are so common in this region. Most colonies of *Pteropus* in Malesia are situated near the sea, and when they are situated inland the animals travel every night to the sea, unless there is a more attractive crop in the interior.

Such a migration (for the sake of the fruits of *Fagraea fragrans*) has been described by CORNER (1940, p. 425).

I possess no data on migrations of other fruit-bats from S.-Asia. We know that *Cynopterus* was already numerous on Krakatau in 1919. In tropical America such migrations seem possible as they have already been described there for flower-bats (cf. VAN DER PIJL, 1956*b*). In Africa the bat *Eidolon helvum* (feeding partly on flower-nectar, partly on fruits) migrates over an unknown distance. Mr. J. B. Hall from Cape Coast (Gold Coast) wrote me on the periodical appearance (medio August—medio October) of large flocks when there was maximum fruiting in the extensive plantations of *Azadirachta indica.*

As has been set forth (VAN DER PIJL, 1956*b*) for flowers and nectar-bats, a stable association between plants and fruit-bats can be reached only when all the year round suitable fruits are available. This should be checked up on islands with a bat population that does not migrate.

BAKER and BAKER (1936) gave a dietary calendar for *Pteropus* in the New Hebrides. This is, however, not an analysis of a natural vegetation as but few wild plants, especially few from the seashore, are included. Many plants mentioned by them are introduced ones.

The plants mentioned in Table II are of old known as sea-dispersed by means of floating seeds or kernels, which partly explains their occurence near the sea. They have, however, bonds both with the sea and with fruit bats, being diplochorous. We may say that their distant dispersal over larger stretches is brought about by sea currents, but their inland colonization by bats.

The question which mode of dispersal is the original one can be answered definitely that zoöchory developed first. Their taxonomic affinity with true zoöchores, as well as the presence of hard layers, as a primarily zoöchorous character, and the structure of their crown (cf. p. 305) favour this conception. One might be inclined to assume that transport by sea-currents would be one of the oldest forms of dispersal, but the fact that sea-dispersed plants form taxonomically a heterogenous group (cf. RIDLEY, p. 250) makes this very improbable. Pacific floras show few signs of speciation from immigrants arrived by sea. This stands somewhat in contrast to the opinion which GUPPY (1906, p. 134) brought forward, with regard to islands floras. He thought that in islands the littoral species would have given rise to part of the inland species or that both are of independant origin. According to him two thirds of the genera of beach plants would have no inland species at all. To this group he reckons even genera like *Vigna*, *Calophyllum*, *Morinda*, *Cordia*, *Ipomoea*, *Casuarina*, *Erythrina* and *Ochrosia*.

In *Hernandia* the loose, inflated calyx that is edible, is a most remarkable adaptation.

Ridley knew the bat-dispersal of *Terminalia catappa* and of *Calophyl-*

lum inophyllum and mentioned (p. 265) also *Ximenia* as diplochorous (birds and see-currents).

It is, however, remarkable that the presence in our group of fruits provided with a fleshy cover that is thin, green and hard, but edible for bats, has as a rule been overlooked. Schimper mentioned it in 1891 in his classical study: "Die Indo-malayische Strandflora" (p. 75). He observed the regular disappearance of this layer before the fruits were dropped, but could not find any function for it.

Guppy (1890, 1917), who paid in his classical researches so much attention to those seeds and their sea dispersal, only says (1890) that the *Morinda* fruit is eaten by sheep, deer and fowl. He ignores the fleshy calyx of *Hernandia*. For the group as a whole he thought that the fleshy covering was functionless and that there was only dispersal by sea, when the fleshy layer had decayed after the fall. In this way he explained the lack of the flesh in most of the floating fruits.

In his study of 1906 Guppy (p. 122) pointed out that a number of sea-dispersed fruits still have bonds with birds. Though he described (p. 152) that a captive cassowary dispersed the externally juicy, large fruits of the undoubtedly diplochorous *Ochrosia parviflora*, he thought, that any other agency of dispersal but that of the sea currents was here out of the question. Strange as it sounds, he practically ignored the role of bats and expressed only some queer ideas, viz. (p. 321) that when visiting the flowers of *Freycinetia* they might carry off the seeds in their fur whilst brushing past a ripe-fruit-head, a misconception repeated (p. 343) in his remarks on *Metrosideros polymorpha*.

Some of the fruits for which he accepts only sea dispersal are very palatable, pure bat fruits, like *Mammea americana*, *Andira inermis* and *Chrysobalanus*.

I described (1936) the diplochory of some of these plants (*Terminalia*, *Morinda*, *Calophyllum*, *Hernandia*) after a visit to a small island in Street Sunda, where I saw actual dispersal by bats.

Docters van Leeuwen described these and other cases from Krakatau (*Cycas*, *Guettarda*, *Pandanus*, *Spondias* and probably *Ximenia*) in his important book on this island (1936). In Krakatau the quick inward spread of *Terminalia* after 1919, following the arrival of *Cynopterus* was very striking.

The diplochory of *Pandanus* is especially well expressed in the structure of its fruits. It has been clearly described and figured in the study of Brown (1931) on the Marquesas. The basal part of the mesocarp is edible flesh containing pectine, sugar and starch (also eaten by man), whereas the apical part of the mesocarp forms the dry floating tissue. Brown even saw that in the shore species the floating part is dominant, whereas in inland species the fleshy part is better developed.

In the older literature the inland dispersal of such plants was often ascribed to crabs and rats, whose activity is mostly destructive, but may play a role (cf. Ridley). Introduced ruminants and pigs may also play a part.

3. *Pacific islands and fruit bats*

The conclusions arrived at in the preceding chapters can be checked up in Hawaii—a tropical island without fruit-bats. In the vegetative sphere it is tropical, but it has a biotically not completely tropical environment. At a former occasion (1936*b*) I already pointed to the scarcity of cauliflory in Hawaii.

Though the total number of indigenes is limited, so that the value of negative finds should not be over-estimated, it is nevertheless remarkable that the Hawaiians had not developed a single table fruit that is native to the region. Their famous *Eugenia malaccensis* is an introduced species. There are no large fruits edible for man in the islands. Of the diplochores discussed in chapter E. *Morinda* is mentioned as growing spontaneously only near the sea. How the spontaneous dispersal of the inland *Pandanus* species takes place is not clear.

The S.-Polynesian region too has no or but few fruits edible for man, and has no fruit-bats.

This becomes the more clear by the simultaneous disappearance of the fruit-pigeons, which obscure the issue elsewhere in many large seeded species of *Sterculia*, *Elaeocarpus*, *Myristica*, *Canarium*, *Sideroxylon*.

It seems attractive to look for a further relation between the eastern limits of resp. the *Megachiroptera* in the Pacific (see map) and the chiropterochorous plants in the islands—just as I did (1956*b*) for bat flowers.

The area of the *Pteropinae*, especially of the genus *Pteropus*, is wider than that of the nectar-bats belonging to the *Macroglossinae*. The latter area agrees fairly well with the tropical part of the generally accepted ancient continental boundary.

It is not satisfactory to consider the distribution only statically, i.e. as a remnant of old continental boundaries. For the *Macroglossinae* such a static concept might still seem more or less acceptable, as their presence is firmly connected with that of specific flowers (and vice-versa), so that colonization is, despite their capacity of flight, only imaginable together with that of the plant species they rely on for food. Moreover, there is no information, even from tropical continents, with regard to any migratory capacity of these flower-bats. In this regard they differ from the American flower-bats, the nectarivorous *Microchiroptera*, which do migrate and surpass the limits of the tropics (cf. VAN DER PIJL, 1956*b*).

For the *Pteropinae* a more dynamic view is indicated. Migrations are known for the genus *Pteropus*, not only over land but also over the sea. In this way the genus seems in Australia to have surpassed the limits of the tropics.

This partly temporary, partly permanent, expansion is facilitated by the adaptability of these fruit-bats, viz. their change to some non-tropical fruits and to the squashing of subtropical flowerrs (cf. RATCLIFFE 1931). Moreover, (and this refers to the eastward expansion of the area), *Pteropus* could follow an eastward migration of those food-plants whose seeds were not only spread by it, but also by sea-currents.

The genus *Ficus* becomes less and less dominant towards the East and only some small-fruited (ornithochorous) species reach the Polynesian Islands. In Tonga and Fidji (within the limit) there are still cauliflorous species. The group of typical cauliflorous species found in Malesia (*F. fistulosa*, *F. glomerata*, *F. miquelli*, *F. variegata*) remain (as Dr. Corner kindly wrote me) west of the line Formosa, Philippines, N. Guinea, North Queensland.

Of course the distribution of Ficus is also influenced by the distribution of the gall-insects, and this might even be the most limiting factor.

The existence of the whole family it belongs to (*Moraceae*) is narrowly linked with that of the fruit bats as demonstrated in the table. Its other large genus, *Artocarpus*, seems also to be limited in its distribution in this way. The breadfruit is everywhere one of the best liked foods of the fruit bats. Though wild forms are abundant in Malesia and the genus is essentially Melanesian, it is sometimes considered to be native to Polynesia, where it forms one of the main foods of man. Apart from other arguments this seems improbable because of the absence of fruit-bats in the region.

For *Musa Fehi*, so popular in Hawaii and Tahiti, the same holds true.

The genus *Spondias* and the whole tribe of the *Spondieae*, with representatives in Asia and America, is markedly chiropterochorous. *Spondias dulcis*, so popular in Tahiti and known as Polynesian plum or Tahiti-apple, is probably introduced in early times or may have come there by sea-currents from Malesia; it has no means of dispersal on land outside the bat area.

The same relates to *Inocarpus edulis*, the Tahitian Chestnut.

The exposition given by Drake del Castillo (1893) creates the impression that *Spondias*, *Inocarpus* and other diplochores have spread spontaneously into the interior of Tahiti, and are maintaining themselves there. This seems strange, the more as later authors as Setchell and Merrill denied that these plants are native to Polynesia. Therefore I was glad to receive information on this point from Mr. J. Lehaire (Service de l'Agriculture of Tahiti). Apart from dispersal by water, *Spondias*, *Inocarpus*, *Hernandia peltata* and *Terminalia catappa* do not grow and spread spontaneously in the interior. Their eventual presence there is always due to human agency.

To the contrary a number of chiropterochores, including *Spondias dulcis*, seem to be indigenous or at least to be spread spontaneously in Tonga, Samoa and Fiji, which are inside the area of the fruit bats. Many representatives, especially of the diplochores, live in Guam, which is also inside this area. It may be said that typically bat-linked taxa with few adaptations to other disseminators, show a decrease towards the boundary-line.

The occurrence of fruit-bats, which itself, of course, depends on historico-geographical factors, is at the present time still a factor of importance in the maintainance and change of phytogeographical boundaries in the Pacific. The often mentioned decrease in number of large-seeded plants towards the East is usually interpreted as a consequence of the absence or inadequacy of land bridges. Besides the fruit-pigeons the fruit-bats may be the main realisators in this connection.

I refer here to the study of SMITH (1955), where the chiropterochorous *Cynometra cauliflora* is mentioned as one of the *Leguminosae* and *Polyalthia* as one of the *Annonaceae* terminating in Fiji.

For the geographical relations between certain flowers and nectarivorous bats I gave (1956*b*) some considerations in the same direction. The chiropterophilous genus *Sonneratia* was mentioned there as remaining within the area of the *Macroglossinae*.

As we dispose here of a map I can elaborate this point in one detail, viz. their curious common limit above the deep trough between the Carolines and the Mariannes. This line does not correspond with clear edaphic or climatic differences or with different possibilities in the seed dispersal of *Sonneratia*. The extension into the Carolines seems strange when we see that many zoögeographists consider the Carolines as oceanic islands, outside the ancient continent. The occurrence of macroglossine bats, however, together with native plants from the chiropterophilous genera *Sonneratia*, *Parkia* and *Musa* suggests that these islands may be continental. It is therefore, interesting that other zoögeographists leave the possibility open, that the scarcity of insects, one of the main arguments for the oceanic character, may be secundary and due to the small size of the islands.

Geological evidence shows that the Carolines West of Truk lie within the andesite-line, and may belong to the ancient Australasian continent. The eastern islands (Ponape and Kusaie) were in this connection seen as probably formed near the continental line in eocene times, and may then in early times have obtained continental plants and animals.

An other supposed geological boundary, the sial-line (cf. STEARNS, 1945) lies a little east of the andesite-line and includes all the Carolines.

The occurrence of *Sonneratia* on Iriomote (Riu Kiu Islands), outside the *Macroglossus* area, remains to be investigated. Do we find there a settled community or a loose collection of sterile immigrants?

E. THE STAMP OF THE BAT ON TROPICAL TABLE FRUITS

A short side trip into the field of human relations may be allowed here.

A visit to a tropical fruit stall results in an impression entirely different from the one in a temperate country. Instead of coloured fruits like berries and cherries, that are naturally ornithochorous, one sees there greenish and brownish fruits, that are in nature chiropterochorous. Fruits of *Mangifera*, *Achras*, *Psidium*, *Annona*, *Spondias*, *Artocarpus*, *Musa*, *Lansium*, *Baccaurea*, *Bouea*, *Dracontomelum*, *Stelechocarpus*, *Diospyros*, *Phyllanthus*, *Mammea*, *Persea*, *Cynometra*, *Detarium*, *Averrhoa*, *Aegle*, *Feronia* and *Manilkara* may be quoted as examples.

Colour pictures of fruits from "the colourful tropics" mostly give a false impression by giving undue preference to the few edible ornithochorous fruits, like *Capsicum* and some *Eugenia* species, to non-tropical tangerines and tomatoes and to the exceptional case (of an ecologically questionable character) of *Nephelium.*

Instead of emitting the fresh scent of strawberries, apples, plums, melons and other fruits "designed" for ordinary mammals, it reeks (with the exception of pine-apples) faintly or strongly unfresh.

The stamp of the bat!

This is very typical in the semi-wild *Mangifera foetida.*

We find a rather primitive condition in many tropical fruits; they are but little improved compared to their wild ancestors—this in contrast to European edible fruits that have far outgrown their forefathers. Nevertheless tropical table fruits are strikingly large. Tropical man could base his fruit menu on large bat-fruits, that were already present in a serviceable form.

Europeans new to the tropics, have to leave behind their accustomed preferences and to follow the taste of bats, though in the cultivated forms of, for instance, the manggo and the banana this taste is not, what it used to be in native species, which smell too strongly. Even in the smell of *Psidium*, *Achras*, *Annona*, *Spondias* and tropical *Diospyros* species something has to be overcome at first, not to speak of *Artocarpus champeden* and *A. integra*. The durian and the manggosteen may remain outside our present discussion, as they are suited respectively for elephants and monkeys. No wonder the newcomer starts to prefer a mangosteen, to finish his career with *Artocarpus*, *Durio*, *Morinda* and a semi-wild manggo.

The bat may even be the solution to some of the "witchcraft and mysteries of the East". The explanation of the mysterious "spitting of beteljuice" on a set table may often be simple when we have an open window, a gutter with bats alighting on it and a red fruited *Ficus* in the neighbourhood.

The not less notorious "stone-throwing" when no outsider can be made responsible, can often be explained in the same way, when the "stones" are kernels of *Spondias* or of *Elaeocarpus*. When the "stones" are said to fall vertically through an undamaged roof it is time to look at the beams for bats.

Fruit-bats have long been known as important to mankind, being a pest to fruit-trees. The damage done by them is immeasurable (cf. Ratcliffe, 1931). Accurate knowledge of the food of fruit-bats has also become important since we know that a bat population may be a reservoir of pathogenous microbes and viri. Direct transmission regularly occurs in America by bites of bats whose diet consists partly of fruits. It seems worth while giving more attention to the question whether a virus may be transmitted by means of fruits. Fruits on tropical markets often show imprints of bats' dentures, obviously from trial-bites.

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LIGHT INDUCED ABSORPTION CHANGES IN PHOTOSYNTHETIC ORGANISMS

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(*received February 23rd, 1957*)

The general procedure for measuring photosynthetic difference spectra is to irradiate the sample under study with weak monochromatic light and observe the change of the light transmission induced by a strong "actinic" cross illumination of the cells. A difficulty involved is that the device registering the light transmission should not directly be influenced by the actinic beam or by fluorescence induced by it. The technique we will describe below was designed on the principle that most of the available photosensitive material in the cells can be charged by a strong lightflash of short duration and that the dark restoration reactions then require a finite time (a few milliseconds) for removing the photoproducts (*cf.* Kok, 1956). An interaction of the actinic and the measuring lights therefore can be prevented by separating them in time. This allowed the registration of complete difference spectra, including the long wavelength region.

Apparatus

The set up used is shown in Fig. 1. Monochromatic light left a Bausch and Lomb 10 × 10 cm grating monochromator and was concentrated on a small reaction vessel (ø 5 mm). The transmitted and scattered light was collected by a high aperture lens and concentrated on a small opening in a fixed screen. Behind this opening a red sensitive photomultiplier (Mauer Vp 690 J) was mounted. The light path of the actinic beam was arranged perpendicularly to the direction of the monochromatic beam. A d.c. mercury arc was used and the illuminating system was identical to that used in our earlier flashing light work (Kok, 1956). A spinning (600 RPM) disc (ø 50 cm) provided with two slits (20 × 4 mm) interrupted the actinic light beam, which moreover could be darkened by a separate shutter.

During the moments the reaction vessel was illuminated by the flashes ($\sim 3.10^{-4}$ sec.), small blades fastened onto the disk closed off the small aperture in front of the photocell and thus intercepted all fluorescence and stray light induced by the actinic beam. Immediately ($\sim$ 1 m. sec.) after a flash was extinguished, the photocell was exposed again to the monochromatic beam and stayed so until ~ 1 m. sec. before a new flash came along.

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[1]) Communication No. 156 of this laboratory; 55th communication on Photosynthesis.

If no flashing light is given, the photocurrent will stay as constant as the light output of the monochromator, except for the two brief moments of darkening during each cycle. But if the flashes induce short lived absorption changes, this current will show additional cyclic variations.

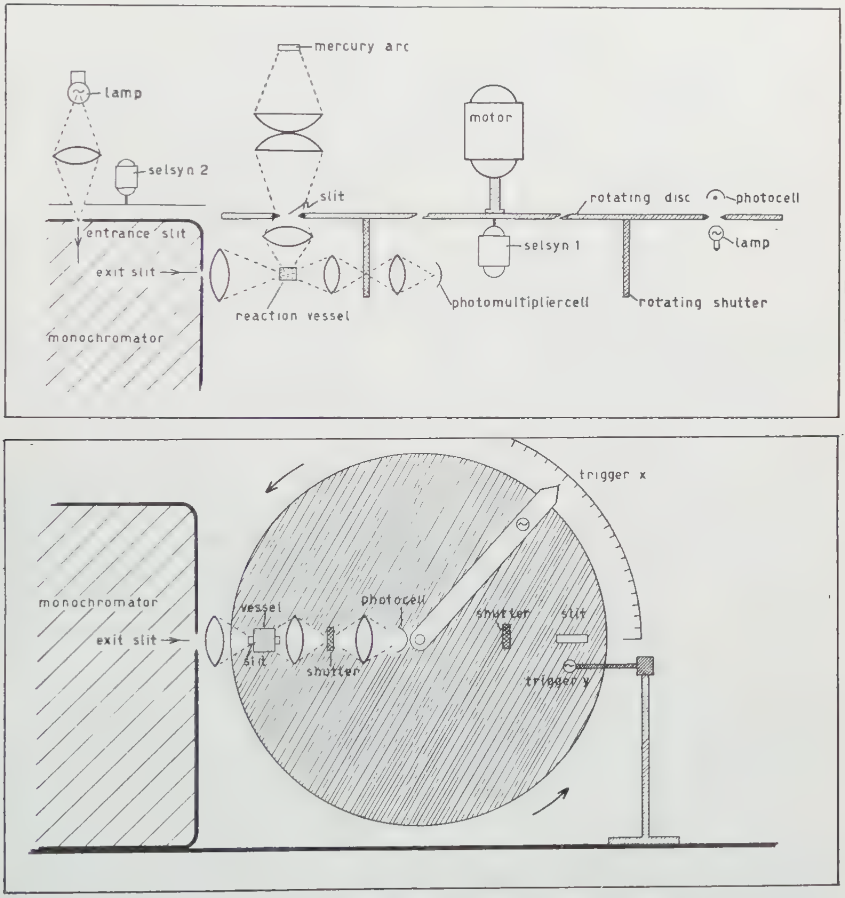

Fig. 1. Schematic drawing of experimental arrangement as viewed from above and from aside. For a further description see text.

The low monochromatic intensity, the inefficient collection of scattered light on the small photocathode and the relatively high noise level of the red sensitive cell made it impossible to significantly observe changes of photocurrent in a single cycle (i.e. in the way Witt, 1955, was able to do with the aid of an oscilloscope screen in his study of the 520 mμ and 475 mμ shifts in green cells). Rather did we have to integrate over a large number of cycles. This was done in the following way (*cf.* Fig. 2): The anode of the multiplier was tied to the input grid of a d.c. amplifier and was at the same time connected to an adjustable compensating voltage (V_1) via a resistor of 2–4 mΩ (determined by the demand for sufficiently fast time response). The photomultiplier output consists of a d.c. component on which the "noise" is superimposed. The compensating voltage was set so as to largely remove this d.c. component and care was taken that the noise component did not exceed the maximum voltage the amplifier could handle with reasonable linearity. The simple three stage amplifier had a gain of 10^4. The average voltage on the cathode of the last tube was compared with a set potential. Any deviation occurring was fed into a Brown recorder, the motor of which actuated a potentiometer correcting the supply voltage (V_2) for the photomultiplier. This servo mechanism automatically compensated for slow drifts of the amplifier, changes in lamp output, settling of algae, etc. (In some experiments it proved to be particularly useful since also long persisting light induced changes of absorption could thus be recorded). The output of the amplifier was split into two identical channels (x and y), which fed the signal via an integrating network into a difference amplifier [1]). The response time of this network could be varied between 5″ and 60″, as dependent on the available effective light intensity (signal to noise ratio). A recorder indicated an eventual difference between the two channels. In addition, both channels were provided with a diode clamp, so that each of them could either be held at a fixed voltage or let the signal pass. Each clamp was actuated via a univibrator, which, if triggered by a brief pulse, opened the channel during an adjustable time interval (usually ∼ 4 m. sec.).

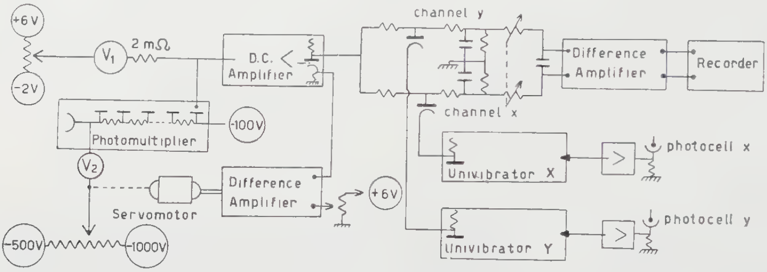

Fig. 2. Arrangement of the electronic circuits described in the text.

In turn each univibrator was actuated by a small size photocell via one stage of amplification. The two photocells were mounted, each opposing a small lamp, close to the spinning disc and actuated the clamp each time a slit passed by. Moreover, one of the photocells (x in Fig. 1) could be swung around the disc circumference and the time location of its triggerpulses in respect to the flashes of the actinic beam could be adjusted at will. The other photocell invariably opened its channel (y) during 4 m. sec. immediately before the flash (i.e. at the end of the darkperiod, when the effect of the preceding lightflash is largely restored). Fig. 3 further illustrates this course of events for the case the first photocell opened its channel (x) immediately after the flash.

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[1]) A description of most of the used electronic circuits can be found e.g. in Elmore and Sands (1949).

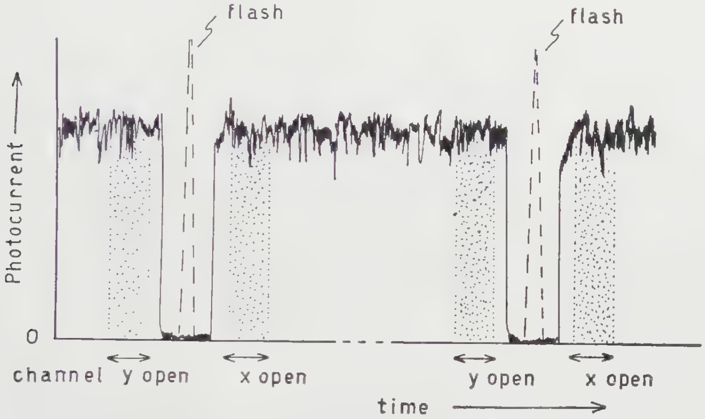

Fig. 3. Illustration of the time course of the photocurrent. Its magnitude during the time intervals y is compared with its value during the intervals x.

If the actinic light is shut off, the two signals, which each influence the difference amplifier during 4 m.sec. per cycle, will be equal and this yields a "zero" reading. If flashes are given, which produce a temporary change of absorption persisting longer than 4 and shorter than 50 m.sec., signal y will differ from signal x. After integration over a sufficiently large number of cycles, a reliable deflection of the recorder will result.

If its photocell is displaced around the disc and channel x opens some time after the flash, a smaller difference will be observed since a partial reversion of the absorption shift has taken place in the meantime. In this way we could measure the time course of the absorption changes.

Finally we may mention the two selsyns shown in Fig. 1: S_2 is governed by S_1 and spins a small disk (at the same speed as the main disk and in the proper phase) in front of the entrance slit. Holes are cut in this disc, which coincide in time with the moments that channels x and y are open. In this way the measuring beam could be made to only illuminate the sample during the required time intervals. The cells then are kept in complete darkness during most of the time and the danger is restricted that the measuring beam would partially prevent the discharge of the photosensitive systems between the actinic flashes (cf. also p. 331).

PERFORMANCE

In addition to the fundamental ones described above, the method has a few technical advantages arising from the fact, that only a single sample, light path and amplifier are used and differences are measured between conditions rapidly succeeding each other. Notwithstanding the poor duty cycle of the detecting system, changes in photocurrent of one part in 10^5 could be observed under not too unfavourable conditions of illumination (i.e. generally over a spectral range of 400–750 mμ).

On the other hand, however, significant measurements of such small effects necessitated a very slow time response or averaging the recorder deflections during several minutes (for both a "zero" and a "light" reading). The effects to be studied were not very constant and moreover do prolonged exposures to the bright flashes produce photoinhibition. Therefore, for a survey of an extended spectral region with intervals of 5 or 10 mμ, exposure times of 30–60″ were used and this sacrifice of sensitivity generally necessitated the use of denser cell suspensions, than those currently used in spectral work.

There is no simple way for directly calibrating the system, but a good approximation can be obtained with the aid of small voltage differences applied between the channels and the known values of input voltage and amplification factor.

We made it a point to always keep the compensating voltage (V_1) constant throughout a spectrum measured with a given sample (or, if necessary, make proper recalculations). Only voltage V_2 was (partly automatically) readjusted for each wavelength setting of the measuring beam. In this way the deflections of the difference recorder could always be expressed as a fraction of a constant photocurrent (cf. Duysens, 1952, p. 70).

Halfwidth of the monochromatic beam was either 7 or 10 mμ.

Results

In Figs. 4–9 we collected a number of observations made with various types of photosynthetic organisms. Changes of photocurrent are plotted vs. wavelength. Some curves represent the average results of 2–4 measurements, which showed only slight mutual variations as long as closely identical samples were used. In the course of prolonged experiments the effects often tended to decrease -possibly due to photoinhibition caused by the intense flashes. A given wavelength (705 mμ) therefore was measured repeatedly in between and used as a reference. In addition, fresh samples were frequently taken.

Fig. 4 shows some data collected with suspensions of green algae of about equal density (20–40 γ chlorophyll/cm^2). The suspension medium contained 0.05 mol bicarbonate buffer pH 8.7 and 0.5 % agar was added in order to prevent settling. The full and dashed curves were obtained with *Chlorella* (strain A and Myers' strain 1410), the dotted curve was obtained with *Scenedesmus* (cf. also Fig. 8) and reproduces part of a spectrum published elsewhere (Kok, 1957).

In the red spectral region the effects show a great variability; in this respect the examples chosen for Fig. 4 represent more or less the extremes of the available data.

One could conclude that at least with our methods of cultivating and resuspending the algae, the 705 peak predominates the other red shifts in *Scenedesmus*. In *Chlorella A* the shift at 650 and in *Chlorella* 1410 the change at 680 mμ tends to be the largest. But pretreatment and suspension density play an important role, as is illustrated with the dashed curve (Fig. 4 top), observed with a pale suspension of (nitrogen starved) *Chlorella A* cells. Here we find three clearly separated peaks of about equal height located at 650, 673 and 700 mμ respectively. As will be pointed out in the discussion of Fig. 8, the occurrence of these three bands might well be considered as characteristic for the difference spectra of green algae.

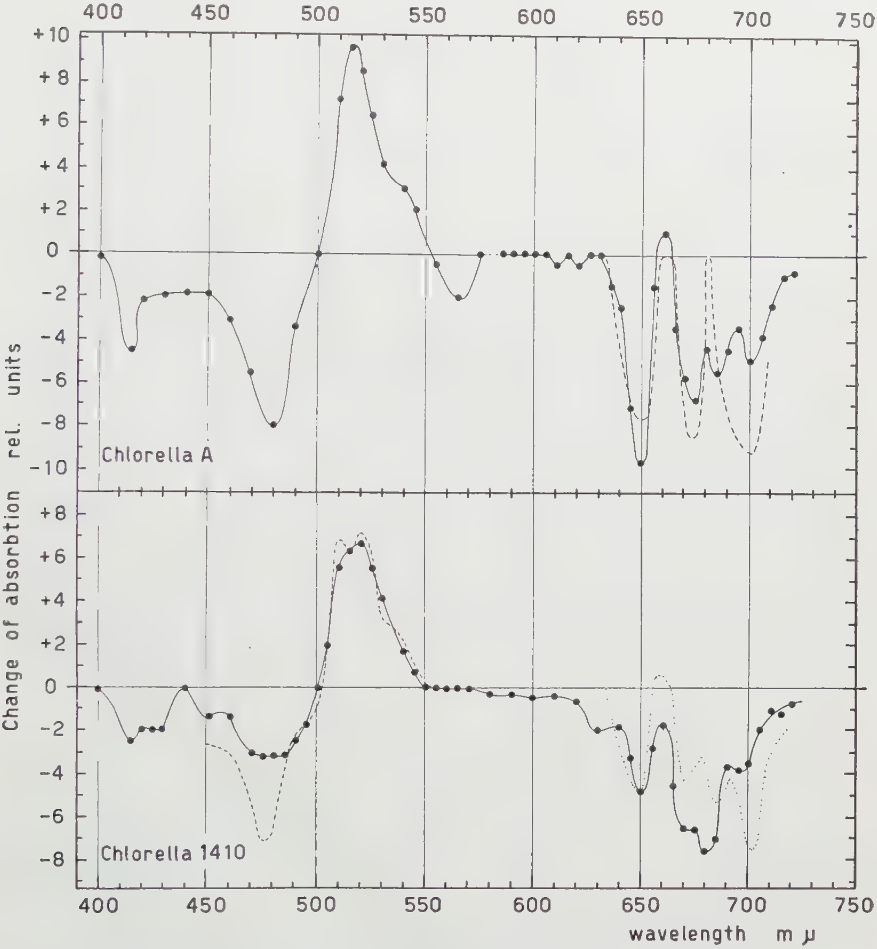

Fig. 4. Difference spectra observed with various green algae.

In the short wavelength region ($\lambda < 580$ mμ), Fig. 4*a* shows data collected with pale, nitrogen starved cells of *Chlorella A*. The ratio between the 520 and the 475 peaks in this case approaches unity and the maximum of the positive change is at 515 mμ. A pronounced shoulder occurs on this band at about 540 mμ. In this experiment a weak negative change is observed between 555 and 565 mμ. In this spectral region the effects appear rather irreproduceable.

One of the examples shown in the left hand side of Fig. 4*b* (*Chlorella* 1410 dashed curve) particularly illustrates the complexity of the positive changes around 520 mμ, where three different maxima can be noticed.

In the blue spectral region we invariably observed negative bands at 475 and 425 mμ, but the deflections eventually occurring in between these two shifts, though doubtlessly significant, were rather unpredictable.

Generally there appears to be very close resemblance between our results and the measurements made in the short wavelength region by DUYSENS (1954), LUNDEGARTH (1954), WITT (1955*a*), STREHLER and LYNCH (1956) and SPRUIT (1956). A decrease of absorption at 650 mμ was also noticed by STREHLER and LYNCH (1956), who used a much slower, but basically similar method as we did for separating the actinic and the measuring beam. The results of COLEMAN, HOLT and RABINOWITCH (1956) are less easily comparable with ours.

Fig. 5 shows results obtained with spinach chloroplasts, which closely resemble the phenomena observed with whole leaves. More than with whole cells, do the data obtained with chloroplasts vary with the pretreatment. Neither are the samples very stable during measure-

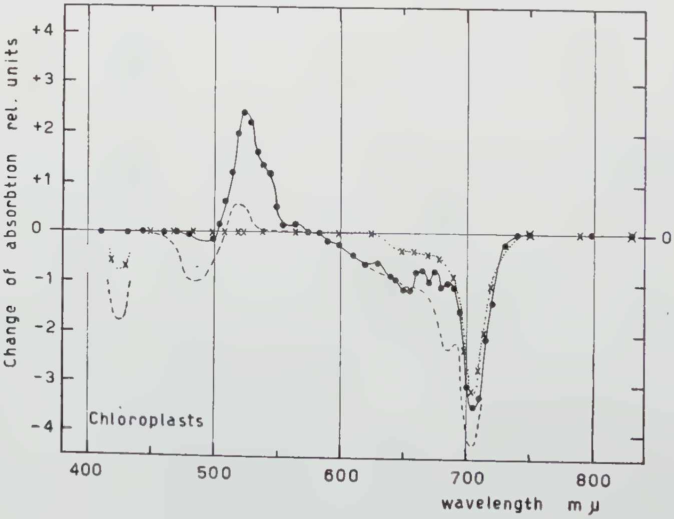

Fig. 5. Difference spectra observed with suspensions of Spinach chloroplasts prepared in different ways.

ments at room temperature. The difference spectra resemble those observed with green algae. The spectrum drawn in full line was obtained with suspensions containing 6 % glucose plus or minus chinon as a hydrogen acceptor. Addition of 2–6 dichlorophenol indophenol (3×10^{-5} mol) left the changes in the red and blue unaffected but strongly decreased the intensity of the 520 mμ band (cf. the dashed curve in Fig. 5). This probably can be correlated with the observation of WITT (1955*b*), that this agent strongly shortens the life time of the 520 change. It then may escape measurement in our apparatus, which requires a lifetime of several milliseconds for detection.

The dotted curve (crosses) shows the peculiar results of a run with the supernatant obtained after low speed centrifugation of a leaf macerate in distilled water. Except for a shift at 425 mμ and a slight decrease of absorption in the red region, only the change around 705 mμ was observed to the full extend. We presently restrict ourselves to the examples given in Fig. 5, which show that a further study of chloroplasts and grana might be quite worthwile.

Fig. 6 gives a difference spectrum observed with the diatom *Nitzschia*, which markedly differs from the ones obtained with green plants.

The decrease of absorption in the blue can be conceived as consisting of two peaks, characterized by maxima at 422 and 436 mμ. The first one probably can be correlated with the corresponding shift observed in green cells.

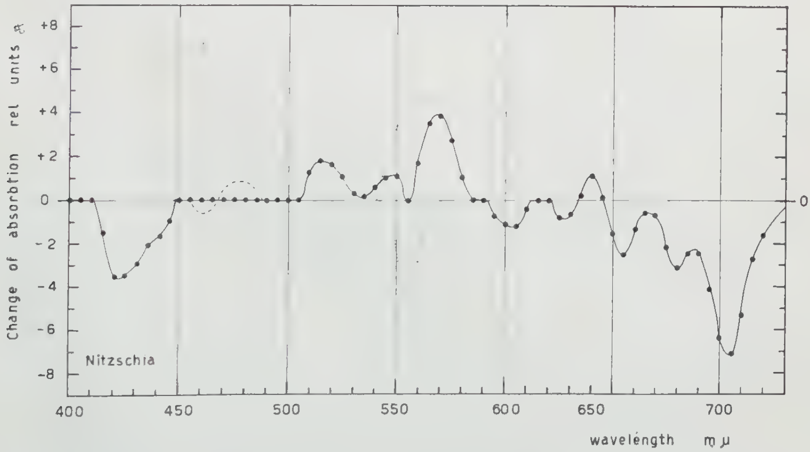

Fig. 6. Difference spectrum observed with suspensions of the Diatom *Nitzschia*.

No negative change was found at 475 mμ; in one experiment the weak changes, plotted as a dashed curve, were observed in this wavelength region. An area of increased absorption, characterized by several maxima, occurs between 505 and 580 mμ. We could tentatively identify the relatively weak band at 515 mμ with the one observed in green plants. Quite typical is the strong maximum at 568 mμ which is further discussed on page 335.

The two dotted curves in Fig. 6 were drawn in such a way that—if added together—the observed curve results. This construction, though, arbitrary, could illustrate the disappearance of a pigment with a narrow absorption band at about 555 mμ and the appearance of a broad absorption band at 565 mμ.

The negative shifts at 605 and 627 mμ and the positive one at 640 mμ were not observed in green algae, also is the location of the negative change at 655 mμ typical. The bands at 680 and 705 mμ, on the other hand, closely resemble the effects observed with green cells.

Fig. 7*a* (top) shows data obtained with pieces of thallus of the red alga *Porphyra;* the negative shifts with maxima at 426 and 705 mμ are quite pronounced both in absolute and relative measure.

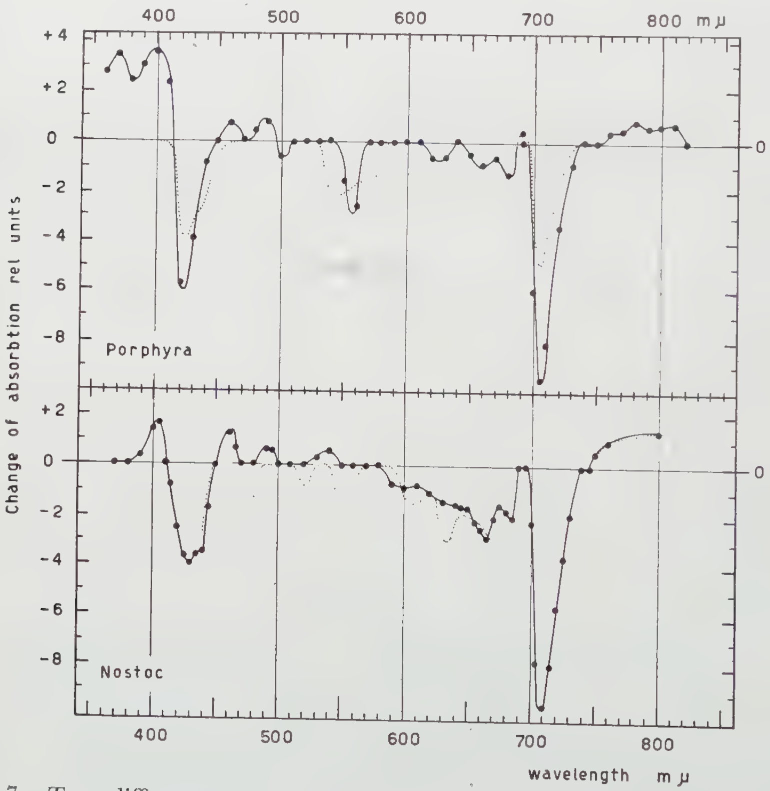

Fig. 7. Top: difference spectra observed with the red algae *Porphyra* (full line) and *Porphyridium* (dotted line). Bottom: difference spectra observed with the blue alga *Nostoc*.

In the blue region this difference spectrum agrees quite well with DUYSENS' (1955) observations made with *Porphyridium*. His interpretation was that transformation of cytochrome f is responsible for the changes at 400, 425 and 555 mμ.

An incidental observation was made with a very dilute suspension of *Porphyridium*, the result is given as a dotted curve in Fig. 7*a*. Noteworth are the broad areas of negative change (410–450 and 530–580 mμ respectively), observed in this experiment. Lack of material so far prevented the collection of further data.

In the red part of the spectrum the 705 change predominates and also its absolute magnitude (approaching a transmission change of one percent) was at least twice the highest values observed even with thick suspensions of green algae and diatoms. The asymmetric shape of the band was discussed earlier (Kok, 1956). Relatively small peaks are observed at 625, 660 and 680 mμ. Zero change is found at 640 and 690 mμ, though at the latter wavelength a possibly significant weak positive change was observed incidentally. Noteworthy is the increase of absorption at wavelengths beyond 740 mμ, extending up to 820 mμ.

This latter increase is also observed in the difference spectrum measured with the blue green alga *Nostoc*, given in Fig. 7 (bottom). The dotted curve in the middle part of this spectrum was derived from another series of measurements. It shows more detailed and pronounced peaks than the full curve, but there is reasonable agreement between the two, if we account for a difference of the zero line. (A change over a broad wavelength area could be involved in one of the spectra).

The intensity of the 708 mμ change is nearly as high as in *Porphyra* and also the other changes in the red region are rather similar. Also the positive effects at 400, 460 and 490 mμ and the negative ones at 425 (400), 475 and 555 mμ can be correlated in both spectra.

INFLUENCE OF SUSPENSION DENSITY

Figs. 8 and 9 illustrate the complications encountered if suspensions of varying density are used. Fig. 8 shows the absorption changes observed with a very dense suspension of *Scenedesmus* (open circles, crosses, dashed curve) in comparison with the ones observed with a very dilute suspension of the same algae (dots and triangles, full line). Since the transmission changes in the thin suspensions were much smaller, the latter data have been multiplied with a factor three for the plots in Fig. 8 (the average photocurrent (V_1) was the same throughout these measurements).

The two spectra differ in several respects: Most noteworthy is the increase of absorption between 730 and 820 mμ, observed with the dense suspension only. The similarity of this change with the ones measured with *Porphyra* and *Nostoc* (Fig. 7) is striking.

The experiments further show how the changes in the blue spectral region tend to fully disappear with increasing density. In the dilute suspension the negative shifts at 425 and 480 mμ are pronounced and approach the magnitude of the 705 shift. In vain did we look

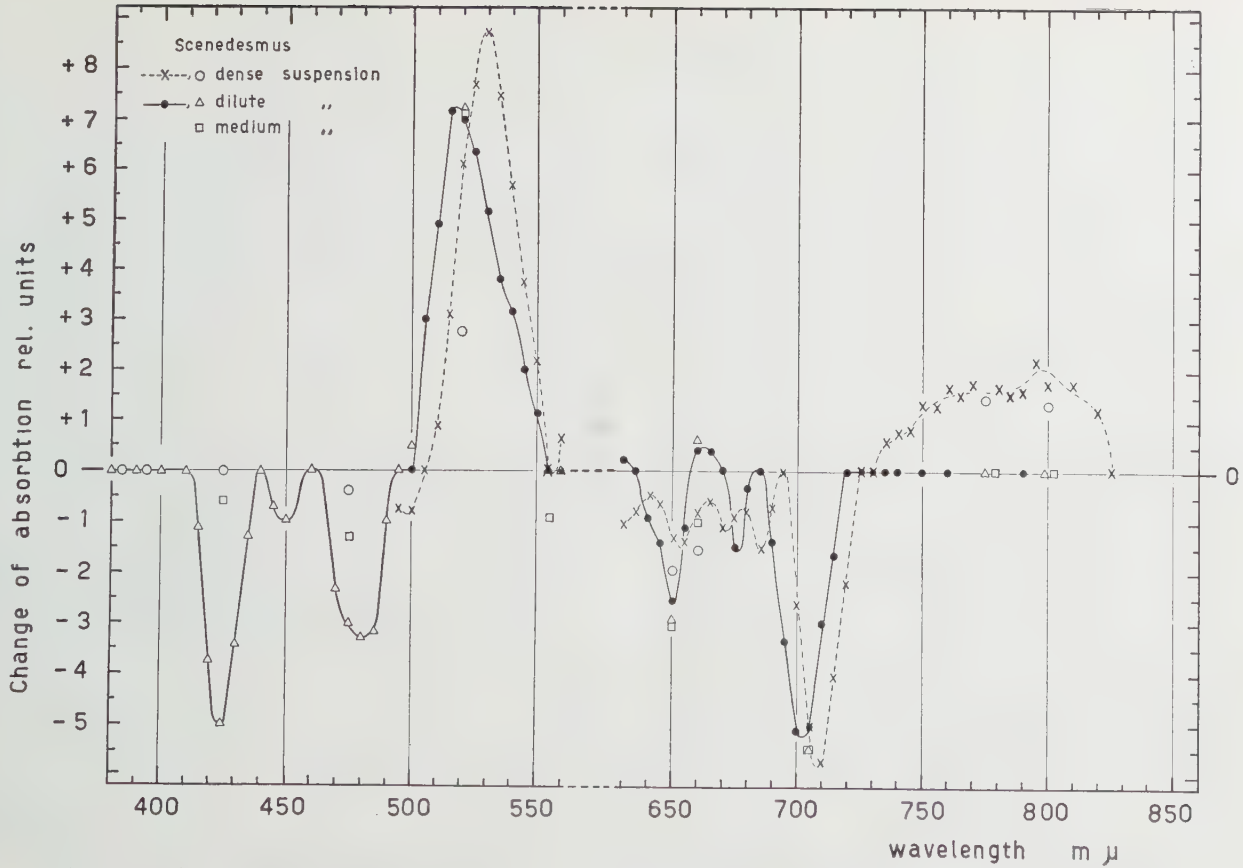

Fig. 8. Difference spectra measured with the green alga *Scenedesmus*, suspended in various concentrations.

for an increased absorption at wavelengths shorter than 400 mμ such as was observed with *Nostoc* and *Porphyra.*

Furthermore, in the dense suspension the blue green band is shifted 12 mμ towards longer wavelengths (from 517 to 529 mμ) as compared with the dilute suspension. In this connection it may be recalled that also in the pale-green suspension used for expt. Fig. 4a this maximum was located at 515 mμ.

The main band in the red is also shifted towards longer wavelengths in the dense suspension (from 703 to 708 mμ) and the other changes in the red differ largely in the two spectra.

Fig. 9 shows data collected with a dense and a dilute suspension of *Nostoc.* The 709 shift had the same shape and location in the two cases (though it was about 3 fold more intense in the thick suspension). But in the blue region did the dilute suspension show far greater changes of transmission—both absolute and relative.

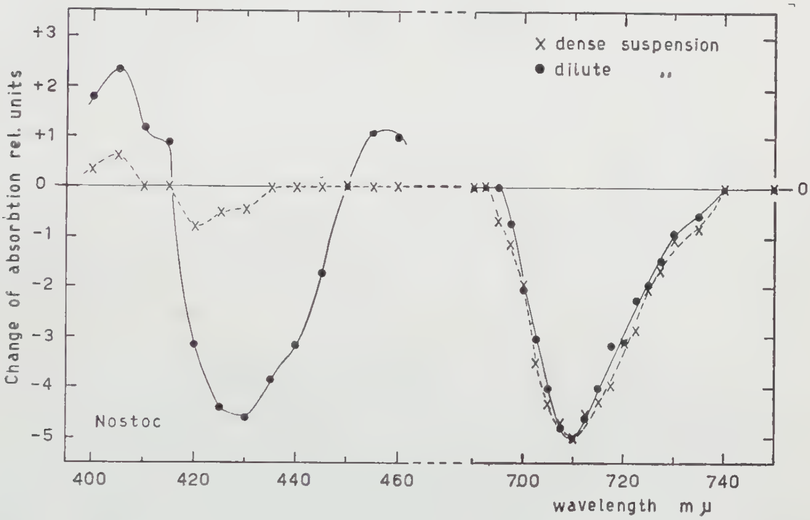

Fig. 9. Difference spectra measured with a dense and a dilute suspension of *Nostoc.*

In dense suspensions, or even in thin suspensions of heavily pigmented cells or chloroplasts, the light absorption may be complete in regions of strong maxima and in extremo only light passing in between algae or reflected by the walls of the reaction vessels will reach the photocathode. A small change in the region of a strong absorption band thus may not be noticed in a too dense suspension. Or, if complete light absorption only occurs in the peak of a shift, the effects may still be noticed on one or both of its shoulders. It thus is feasible that with increasing suspension density a single band of reversible absorption change will be shifted in wavelength location, become asymmetric, or even be split into two bands, located at the sides of the maximum observed in a thin suspension.

On this basis most of the effects of Figs. 8 and 9 in the blue spectral region can be qualitatively understood. The strong absorption by chlorophyll and carotenoids may obscure the 420 and 475 shifts as well as the short wavelength side of the 515 mμ band.

The interpretation of the phenomena in the red is more difficult. In Fig. 8 the dilute suspension showed a negative peak at 676 mμ and zero change at 685 mμ; the dense suspension on the other hand showed a new peak at 685, a minimum of absorption change at 678 and another peak at 671 mμ. This might possibly be an indication that the 676 mμ band is to be ascribed to disappearance of chlorophyll a absorption, which peak in the dense suspension becomes only manifest at both of its shoulders (cf. also the double peaks observed in this wavelength region in the spectra of Fig. 7). This interpretation then could lead one to accept that the 650 mμ band is due to decrease of chlorophyll b absorption (in the dense suspension similar deviations as discussed above are observed). A further consequence of this reasoning then would be that the (often asymmetric) 705 band has to be ascribed to the removal of a separate so far unknown-pigment system. The weak, but significant increase of absorption at 662 mμ indicates that also the formation of new pigment material is involved. Deferring a further discussion of possible interpretations, it should still be remarked that Fig. 8 shows the usefulness suspensions denser than strictly required for sufficient accuracy of measurement. Effects brought about by pigments with a low specific absorption or present in very low concentration could escape observation in too dilute suspensions: the increase of absorption between 725 and 820 mμ is only observed in a dense layer of green algae.

LIFE TIME OF THE ABSORPTION CHANGES

The decay of the effects induced by the flashes could be followed by measuring the change of light transmission in relation to the time location of the observation point succeeding the flash.

For effectively preventing the tails of the flashes to influence the photocell, the shutter on the disc overlapped the flash more than a millisecond on both sides. After the shutter opened the pinhole aperture, the photocurrent had to rise from its dark level to within less than a promille of its final value before significant observations during observation time x (Fig. 3) could be made. Therefore in our present apparatus the first few milliseconds after the flash could not be studied. Measurements could only be carried out at room temperature and a further restriction was that only for the major changes the time course could be studied with sufficient accuracy. Most data were collected with green algae, though other organisms showed practically identical behaviour. A few data are shown in Fig. 10.

It appeared that the various changes showed about the same time course, which closely approached an exponential character over the region we were able to study.

The decay halftimes of 5–8 m.sec. were 2–3 times shorter than the shortest time observed by WITT (1955) for the change at 520 mμ.

WITT's data, collected with a number of dark-and flashtimes (a variation which our set up did not allow) show a decrease of halftime with decreasing flash duration and a deviation from first order decay. No flash regime, directly comparable to ours was used.

Finally it may be mentioned that, when a complete spectrum was measured with observation point x located several milliseconds after the flash, all deflections were proportionally decreased and no indications could be found of additional short living intermediates formed during the dark period as transformation products of those formed primarily by the flash.

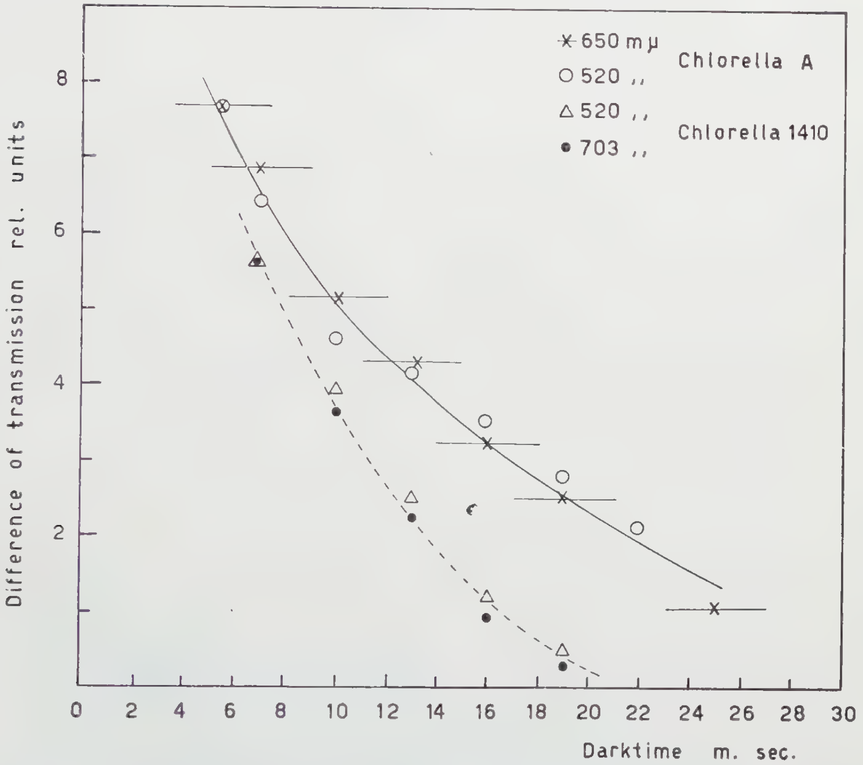

Fig. 10. Time course of the magnitude of the absorption changes as observed at three wavelengths with *Chlorella*.

INTENSITY OF THE ACTINIC BEAM

For the major changes it was possible to study the magnitude of the effects as a function of the intensity of both the actinic and the measuring beam. In Fig. 11 some data, collected in an experiment with *Scenedesmus* are plotted, which show typical saturation curves for the effects. Within the experimental accuracy most changes showed about identical dependency of intensity, except for the 520 shift, which is obviously saturated in much (about fourfold) weaker light.

Evidently the change at 520 has to be ascribed to a system different from the other shifts. This conclusion is further supported by the facts that it is only found in green cells (cf. Figs. 4, 5 and 8) and that it disappears if special acceptors are used in chloroplast suspensions (cf. Fig. 5 dashed curve). It is not possible to decide from the data

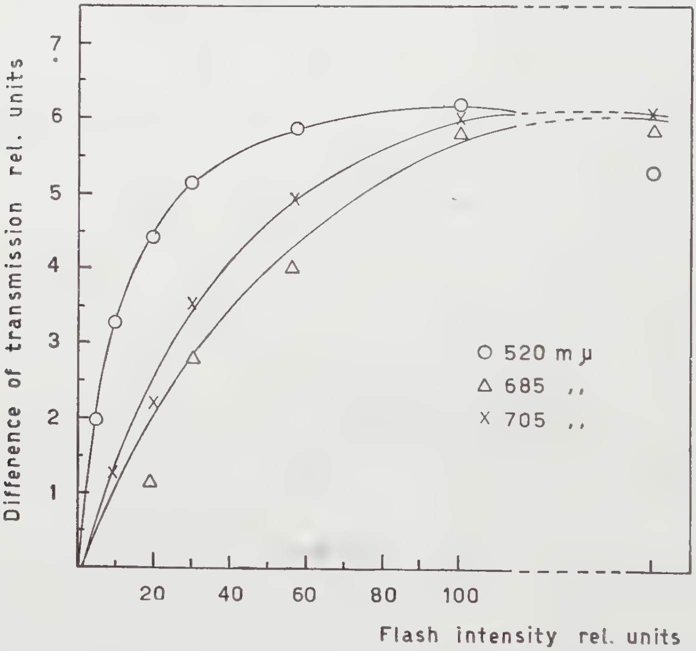

Fig. 11. Influence of the intensity of the actinic light on the magnitude of the absorption changes at three wavelengths observed with *Scenedesmus*.

whether either a different primary light acceptor system is involved or only a separate dark system occurs, driven via the primary reaction responsible for the other changes as well.

In our apparatus the light flashes were induced by the same set up as was used for volumetric oxygen determinations, though the rigorous requirements for separating the two beams necessitated some sacrifice of flash duration and -intensity. Still the intensity requirements for saturating either oxygen evolution per flash or changes of absorption in the red spectral region were of the same order of magnitude. We therefore tend to correlate these changes with the formation and removal of the primary photochemical product(s).

INTENSITY OF THE MONOCHROMATIC BEAM

Theoretically no influence is expected of the intensity of the monochromatic beam as long as it is sufficiently weak to not induce significant absorption changes or to prevent discharge of the acceptor system loaded by the flash.

On the other hand, a monochromatic intensity as high as possible should be used to ensure that the observed variations of photocurrent are caused by absorption changes only and not due to phosphorescence of glass or chemiluminescence of the algae (effects, which would simulate a decrease of absorption):

After traversing the sample, the monochromatic beam of intensity I_m reaches the photocell and yields a preset voltage (V_1) across the 2 mΩ resistor (cf. Fig. 2). Thus, $V_1 = g_m I_m$, in which the term g_m contains the spectral sensitivity and the amplification factor of the photomultiplier cell and therefore varies along with voltage V_2.

Suppose a flash increases the intensity transmitted by the algæ with a small fraction f. I_m, so that after the flash: $V_1' = g_m (1 + f) I_m$. In addition the flash induces phosphorescence, the intensity of which (I_p) will be constant as long as the flash intensity is constant. However, V_2 is dependent upon the density of the sample and the wavelength setting of the monochromator, (determining I_m and thus g_m). The amplification of the multiplier cell thus is a function of wavelength and so will be the signal resulting from phosphorescence: $V_p = g_p I_p$. (Due to the spectral variation of the photocathode response, g_p will generally differ from g_m). Thus: $V_1' = g_m (1 + f) I_m + g_p I_p$. The recorder indicates:

$$V_1' - V_1 = \triangle V = f.g_m I_m + g_p I_p = f V_1 + g_p I_p$$

and the computed change:

$$f = \triangle V / V_1 - g_p . I_p / g_m . I_m \qquad (1)$$

As long as $g_p I_p$, is small enough, the measurements correctly indicate the first term of Eq. (1) only. Since I_p is constant and g_p proportional with g_m at any given wavelength, the second term will become increasingly important if the (transmitted) intensity of the measuring light decreases.

A simple way for checking the interference of luminescence thus is to measure a given absorption change with varying intensities of the measuring beam (V_1 constant). In actual checks, under not too extreme conditions, we found f to be constant within experimental error over a 10 to 20 fold range of I_m. With dense suspensions, however, a distortion of the difference spectra is not fully excluded in regions of strong absorption peaks.

Since obviously the two discussed aspects put controversial demands on the intensity of the measuring beam, we arranged the extra rotating disc in front of the entrance slit of the monochromator (cf. Fig. 1). Relatively strong monochromatic light thus could be used during the observations without great danger of annulling the effects of the flashes. The effect of this extra arrangement, however, proved to be only slight.

Significance of the effects

One could wonder whether the small effects brought about by the high intensity-flashes are correlated with truly photochemical reactions.

Scattered light contributes appreciably to the illumination of the photocathode and the temperature increment of the chloroplasts, induced by the flashes, could induce a slight re-arrangement of the pigment molecules (cf. Shibata, 1955). In this respect we may also point to some striking similarities in the location of maxima in difference spectra and in the data of Goedheer (1955), and Latimer and Rabinowitch (1956), concerning birefrigence and selective scattering of green cells.

In this connection Fig. 12 illustrates how the changes in the red observed in expt. Fig. 8 (dilute suspension) could, for instance, be conceived as mainly consisting of slight shifts of two absorption maxima (normally located at 658 and 691 mμ and shifting 3 mμ in opposite directions), but then a considerable change especially of the width of the long wavelength peak also has to be accepted.

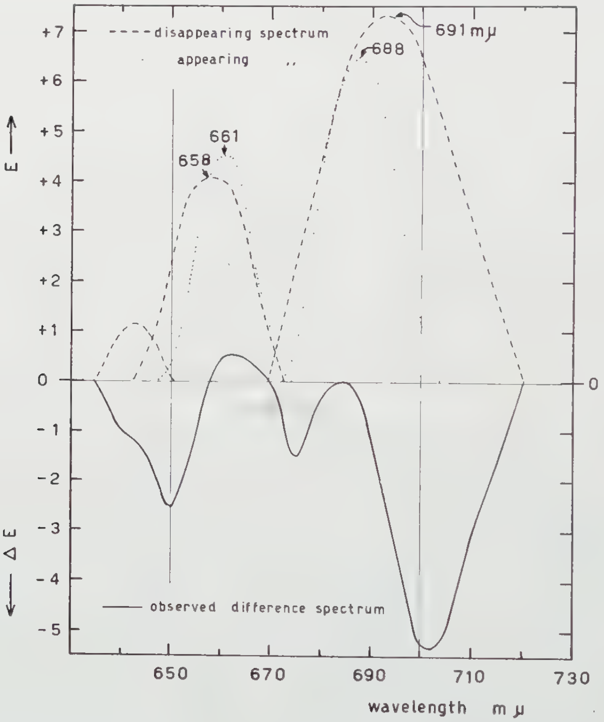

Fig. 12. Possible analysis of part of the difference spectrum given in Fig. 8 (full line).

An argument against this interpretation is that the effects disappear or become quite different after the cells are damaged by heat, cold-treatment or poisoning (cf. also Witt *l.c.* and Spruit *l.c.*).

Another argument for correlating the described absorption changes, at least partly, to photochemical changes of pigment molecules is, that similar phenomena can be observed *in vitro*, i.e. with true solutions of chlorophyllous pigments. As an example—merely presented here to illustrate this point—Fig. 13 (open circles) shows a "difference" spectrum, observed in our apparatus with an oxygen free solution of pheophytin a in pyridin to which small amounts of ascorbic acid and thiouria were added. Similar data could, e.g. be obtained with clear solutions obtained by grinding spinach leaves directly in ascorbic acid containing pyridin, as is shown with the dotted curve in Fig. 13. In some respects—such as the decrease of the red and blue absorption peaks and the appearance of new absorption bands in the ultra violet and the infrared, these data qualitatively resemble observations made with living cells.

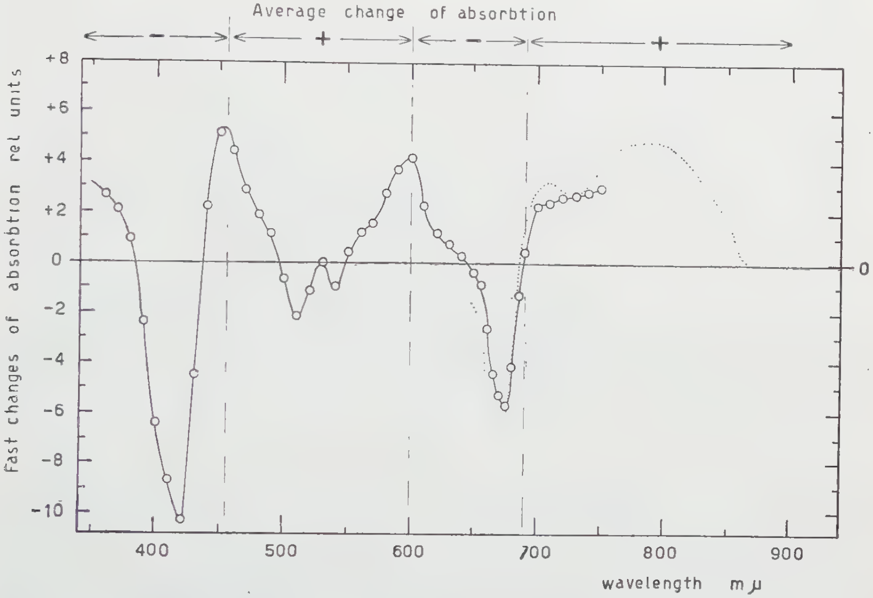

Fig. 13. Examples of "difference spectra", observed *in vitro*. The spectral areas over which the average absorption value slowly increased or decreased are also indicated (top).

It must be stated, however, that Fig. 13 is chosen from a number of experiments of preliminary character, which yielded rather complex and variable results. In addition to truly reversible fast absorption changes our apparatus will also respond to unidirectional changes, which are induced stepwise (flash after flash). If such a progressive absorption change occurs, the average photocurrent will vary and this may yield a measurable deflection of the servo mechanism readjusting voltage V_2 (also a recording instrument).

With living material such deflections were not observed, which proved that we were dealing with reversible transformations mainly. In *in vitro* experiments strong deflections could occur, which, if in the same direction as the step by step changes pointed to the occurrence of unidirectional transformations. If, on the other hand, the two deflections had opposite signs, more complex phenomena were obviously involved. A still further complication is that in various spectral regions the deflections of each or both of the two recorders may change in sign and magnitude in the course of the reactions (which ultimately result in bleaching of the material).

A further discussion therefore is better delayed until more quantitative data are available, for which purpose an improved technique is designed. We may, however, point to an obvious similarity between the spectral dependency of the "average" changes of expt. Fig. 13 with the changes observed by LINSCHITZ and RENNERT (1952) after illuminating chlorophyll in rigid solvents.

DISCUSSION

The described difference spectra of various plant types do not show great uniformity. Generally observed effects occur only in the far red and at 425 mμ. The red shifts point to a role played by chlorophyllous pigments, but probably none of the known chlorophylls is characterized by a main blue absorption band at 425 mμ *in vivo*. One could speculate that this band is correlated with the same pigment, responsible for the change at 705 mμ. The location of the red absorption maximum of this hypothetical pigment might suggest that it acts as the final light trap in photosynthesis.

On the other hand, the complex phenomena characterizing the energy transfer processes in red and blue algae (cf. HAXO and BLINKS, 1950 and DUYSENS, 1952) and the sharp drop of the quantum yield at wavelengths beyond 680 mμ, observed in all types of organisms studied by EMERSON and LEWIS (1942, 1943) and TANADA (1951) could indicate that the function of this pigment—or part of it—is more involved.

The absorption changes at 440 mμ and those at, or around, 678 mμ can be correlated with the disappearance of chlorophyll a. Similarly, chlorophyll b might be involved in the relatively large changes observed at 475 and 650 mμ in green cells.

But, as was discussed earlier, (cf. Fig. 12 and also KOK, 1957) the complex changes in the red still can be interpreted in different ways. For instance, the two negative shifts in fig. 8 (dilute suspension) at 650 and 675 mμ enclosing a positive change at 663 mμ could be ascribed to a single pigment, normally characterized by an absorption maximum at about 663 mμ. If the light flashes caused this band to become narrower and at the same time more intense, a difference spectrum as observed would result. One could use a similar interpretation for the three shifts observed with *Nitzschia*, located at 625 (—), 640 (+) and 655 (—) mμ respectively. (Such a reasoning is supported by the fact that the absorption spectrum of this organism shows a distinct peak at 640 mμ due to absorption by chlorophyll c cf. WASSINK and KERSTEN, 1946).

In the same wavelength region, also *Porphyra* and *Nostoc* showed bands of decreased absorption. The absorption spectrum of *Nostoc* is characterized by a predominant maximum at 620 mμ (in *Porphyra* this maximum is less pronounced). We therefore are inclined to correlate the absorption shifts in this region with changes in phycocyanin (the dotted curve of Fig. 7*b* shows two maxima at both sides of 620 mμ). It may be recalled (cf. p. 000) that the only run we were able to make with a dilute suspension of *Porphyridium* showed a broad band of decreased absorption between 530 and 580 mμ, possibly due, at least partly, to disappearance of phycoerythrin.

We would like to discuss in slightly more detail the possible role played by carotenoids. The changes at 475–520 mμ in green plants were studied by several workers and accepted as due to the transformation of a single pigment of unknown character. From our data it appears that these bands, typical for green plants, may not be correlated. Only in *Nitzschia* is a small positive change observed at 520 mμ, which might correspond to the one found in green cells. In this organism there is a pronounced additional band of positive change at 560 mμ (cf. Fig. 6 full and dotted curves). This latter peak is located on the long wavelength wing of the fucoxyanthol absorption band. One could ascribe all or part of the observed changes between 510 and 580 mμ (except the 555 shift) in *Nitzschia* to a complex transformation of this carotenoid (cf. Kok 1967 b).

In analogy with the phenomena observed with diatoms, it seems likely that the 520 bands in green cells have to be correlated with transformations of carotenoids.

Finally we may mention the role played by cytochromes. If Duysens' (1955) interpretation of the blue shifts observed in red algae is correct, it might follow that the generally observed band at 420 mμ is due to the oxidation of cytochrome f. However, the expected increase of absorption at 410 mμ, due to the formation of the ferricytochrome, is observed in blue and red algae only (cf. Fig. 7).

A decrease of absorption at 555 mμ—which could indicate the disappearance of the α band of this cytochrome—was distinctly observed in *Porphyra*, but in red algae also phycoerthrin may be responsible for changes in this spectral area. Changes at 555 mμ have been observed in all organisms which we studied, but the effects were rather irreproduceable. An increase of absorption was found in several cases at 565 mμ, which could be due to the appearance of the α band of ferrocytochrome b.

If our rather ad hoc attempts to correlate the various absorption changes with known plant pigments are justified, it is striking that practically all these pigments can be involved.

SUMMARY

Reversible changes of absorption, induced by flashes of strong light were studied in various photosynthetic organisms. The technique used allowed to include the red and infrared spectral regions into this study. In the short wavelenght region the results showed good agreement with earlier observations largely made with continuous actinic illumination. Though significant differences between various types of plants appear to exist, a decrease in absorption in the red region, characterized by several maxima, was generally observed, the most pronounced effect occurring at 705 mμ. An increase of absorption was observed between 720 and 820 mμ.

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MYCOSPHAERELLA JOERSTADII AUF RUBUS CHAMAEMORUS

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(*eingegangen am 22. Februar 1957*)

Vor einiger Zeit erhielt ich von Herrn Ivar Jørstad vom Botanischen Museum in Oslo einige Blätter von *Rubus chamaemorus* L. Diese ursprünglich von Herrn Gunnar Sandved von der Agricultural Experiment Station Holt bei Tromsø stammenden Blätter waren teilweise in grünem Zustande gesammelt, teilweise im Freien unter dem Schnee auf Moos liegend überwintert.

Rubus chamaemorus hat in den nördlichen Teilen von Skandinavien als Lieferant einer wertvollen Beere einige Bedeutung. Weit verbreitet findet sich auf den Blättern eine Blattflecken-Krankheit unbekannter Ursache. Die Blattflecken sind unregelmässig, rundlich oder eckig. Besonders blattoberseits sind sie sehr auffallend. Sie sind 1–4 mm gross, weisslich verbleichend und von einem 2–3 mm breiten, purpur- oder braunroten Saum umgeben. Blattunterseits treten sie als unscharf begrenzte, schwache Verfärbungen wenig hervor. In diesen Blattflecken konnten während des Sommers keine Fruktifikationen irgend eines Pilzes gefunden werden.

In den von Gunnar Sandved unter Schnee überwinterten und dann am 15. Mai nachgeprüften Blättern wurde eine *Mycosphaerella* gefunden, die sich als neu erwies und die hier beschrieben werden soll:

Mycosphaerella Joerstadii v. Arx spec. nov.

Perithecia semper hypophylla, solitaria vel complura aggregata, subepidermalia, nigra, globosa, 80–130 μ diam., collo plano vel papilliformi erumpentia, pariete pseudoparenchymatico, nigro, 10–18 μ crasso, e cellulis crassiuscule tunicatis, nigris, 7–20 μ diam. composito. Asci sat numerisi, cylinderaceo-clavati, crassiuscule bi-tunicati, brevissime stipitati, 8-spori, 45–58 × 8–12 μ. Ascosporae plus minusve distichae, oblongae vel clavatae, utrinque attenuatae et rotundatae, plerumque rectae, circa medium septatae, vix constrictae, hyalinae, 15–19 × 3.5–4.5 μ. Paraphysoides nullae.—Ad fol. sicc. Rubi chamaemori, Norvegia, prope Tromsø.

Auf der Unterseite der überwinterten Blätter sind die Perithecien als kleine, schwarz glänzende Pünktchen sichtbar. In den alten Blattflecken entwickeln sie sich in kleineren oder grösseren Herden unter der Epidermis im Schwammparenchym, sind kugelig oder etwas niedergedrückt und 80–130 μ gross. In der hervorbrechenden, papillenförmigen, erst völlig geschlossenen Mündung öffnen sie sich bei der Reife mit einem unregelmässigen Porus. Ihre Wand ist 10–18 μ dick und besteht aus 2–3 Lagen von derb- und fast schwarzwandigen, eckigen, etwas flachen, 7–20 μ grossen Zellen. Die einem flachen, hyalinen, kleinzelligen Basalpolster ziemlich zahlreich aufsitzenden Asci bilden eine dichte Rosette. Sie sind zylinderisch, oben breit abgerundet, unten knopfig gestielt, 45–60 × 8–12 μ gross, besitzen eine doppelte Membran und enthalten 8 Sporen. Diese sind oblong, zylinderisch-keulig, in der Mitte septiert, kaum eingeschnürt, hyalin und 15-19 × 3.5–4.5 μ gross. Paraphysoiden sind keine vorhanden; jung sind die Gehäuse von hyalinen und farblosen, rundlich eckigen Zellen erfüllt, die von den heranwachsenden Asci nach oben gedrängt und resorbiert werden (vgl. Abb. 1).

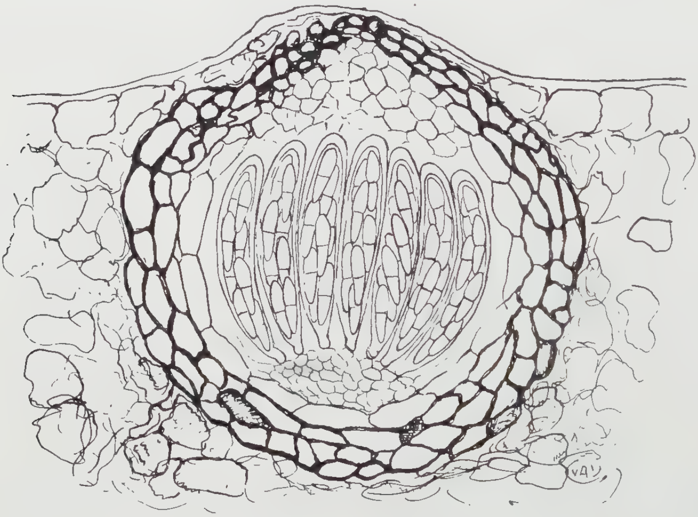

Abb. 1. *Mycosphaerella Joerstadii*, Schnitt durch ein Perithecium. Vergr. 500 mal.

An den Blattstellen, wo hypophyll die Perithecien hervorbrechen, lassen sich epiphyll die Umrisse der Blattflecken noch deutlich erkennen. Es ist daher wahrscheinlich, dass *Mycosphaerella Joerstadii* die Ursache der oben erwähnten Krankheit ist. Sicher bewiesen werden kann dies aber nur durch die Herstellung von Reinkulturen und durch Infektionsversuche.

Auf *Rubus chamaemorus* war bisher eine *Sphaerella*, nämlich *Sph. chamaemori* Karst. bekannt geworden. Diese wurde ebenfalls auf einigen Blättern des von Jørstad erhaltenen Materials gefunden und soll unten noch ausführlicher besprochen werden.

Mit einer der auf anderen Rubus-Arten beschriebenen *Mycosphaerella-* (*Sphaerella-*) Arten lässt sich *M. Joerstadii* nicht identifizieren. Am ehesten würde sie noch zu *M. rubi* Roark passen. Diese Art wurde von Roark (1921) als Ascusform von *Septoria rubi* (Duby) Westend. beschrieben und unterscheidet sich von *M. Joerstadii* durch kleinere, nur 60–80 μ grosse Perithecien und durch längere, 20–25 × 3.5–4.25 μ grosse Ascosporen. Möglicherweise ist sie von der in Japan auf toten Blättern von *Rubus spec.* gefundenen *M. minoensis* Syd. (Sydow, 1913) nicht verschieden.

Sphaerella ligea Sacc. (Syll. fung. *1*, 483), *Sph. rubicola* McAlp. (Syll. fung. *17*, 637) und *Sph. rubina* Peck (Syll. fung. *14*, 527) zeichnen sich durch ungefähr 7 μ breite Ascosporen aus. *Sph. ligea* könnte nach der Diagnose beurteilt eine Form von *Mycosphaerella tassiana* (de Not.) Joh. = *M. allicina* (Fr.) Vestergr. sein (vgl. von Arx, 1949), die beiden andern Arten könnten zu *Didymella*, *Sph. rubina* z. B. zu *D. applanata* (Niessl) Sacc. gehören.

Die auf Stengeln von *Rubus idaeus* beschriebene *Sph. fructicum* Starb. (Syll. fung. *9*, 643) unterscheidet sich von *M. Joerstadii* durch kleinere Ascosporen, die nur 9–10 × 3 μ gross sein sollen. *M. dubia* Wolf hat ebenfalls kleinere, nur 11–14 μ lange Sporen und wurde von Wolf (1935) als Ascusform von *Cercospora rubi* Sacc. beschrieben.

Auf einigen der von Jørstad erhaltenen, überwinterten Blätter wurde ein weiterer Ascomycet gefunden. Dieser liess sich mit *Sphaerella chamaemori* Karst. identifizieren. Von dieser Art konnte eine Probe des Originalexemplares aus dem Herbarium in Helsinki

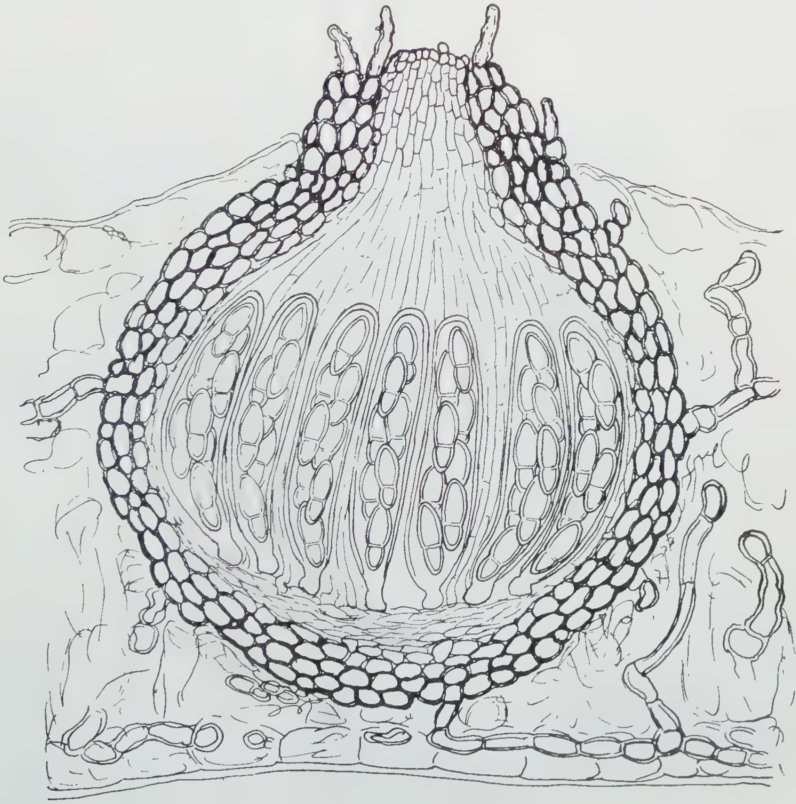

Abb. 2. *Venturia chamaemori*, Schnitt durch ein Perithecium, entworfen nach dem Originalexemplar von *Sphaerella chamaemori*. Vergr. 500 mal.

untersucht werden. Bei ihr handelt es sich um eine fast borstenlose *Venturia* sensu Sacc. (vgl. MÜLLER und MENON, 1955; KORF, 1956), die als **Venturia chamaemori** (Karst.) v. Arx comb. nov. (Syn.: *Sphaerella chamaemori* Karst.—Mycol. Fenn. *2*, 173, 1873) eingereiht werden kann. Dies geht aus folgender Beschreibung hervor:

Die herdenweise zerstreut dem Blattgewebe tief eingesenkten Perithecien brechen epiphyll oder hypophyll mit einer kegelförmigen, 45–60 μ breiten und ebenso hohen Mündung hervor. Setae fehlen oder sind nur spärlich rund um den 25–35 μ weiten Mündungskanal als 20–40 μ lange und 5–7 μ breite, knorrige Hyphenenden ausgebildet. Die Perithecien selbst sind kugelig und 100-160 μ gross. Ihre Wand ist 10–15 μ dick, braun und besteht aus 3–4 Lagen von rundlich eckigen, etwas abgeplatteten, 9–14 μ grossen Zellen. Die parallel stehenden Asci sind zylinderisch, oben abgerundet, nach unten etwas verbreitert und dann in einen kurzen, knopfigen Stiel verjüngt. Sie besitzen eine doppelte, 1–1.5 μ dicke Membran, enthalten acht Sporen und messen 55–80 × 10–15 μ. Die Sporen sind länglich ellipsoidisch, etwas unter der Mitte septiert und eingeschnürt, bräunlich oder olivengrün, 15-20 × 6–8 μ gross. Die reichlich vorhandenen Paraphysoiden sind fadenförmig, zellig gegliedert, 2–3 μ dick, hyalin und vor allem über den Asci miteinander verwachsen oder verklebt (vgl. Abb. 2).

Das Substrat ist von einem braunen Hyphengeflecht durchsetzt, das aus reich verzweigten, septierten, knorrigen, oft anschwellenden, 4–6 μ dicken Fäden besteht. Durch dieses Mycel sind die vom Pilz durchwucherten Blattpartien dunkler verfärbt. Zwischen Kutikula und Epidermis bildet er hie und da auch ein dünnes Häutchen von mehr oder weniger radiärer Struktur.

SUMMARY

In Scandinavia the leaves of cloudberry (*Rubus chamaemorus* L.) commonly show leaf spots. Fungus fructifications are never seen on the spots during the summer. On leaves overwintered under snow near Tromsø (Norway), perithecia of a *Mycosphaerella* species appeared on the old spots in spring. This fungus is described under the name *Mycosphaerella Joerstadii* v. Arx spec. nov. On some leaves, another fungus is found, which was proved to be identical with *Sphaerella chamaemori* Karst. and which has to be named *Venturia chamaemori* (Karst.) v. Arx comb. nov.

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NOVITATES VOCHYSIACEARUM II

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(*received February 22nd, 1957*)

1. **Vochysia lanceolata** Stafleu, Tropical Woods 102: 49. *fig. 1.* 1956 (*descr.*); (this publication fig. 1*a* and *b*).

Vochysia sectio *Ciliantha* Stafleu, subsectio *Ferrugineae* Warming. A *V. vismiifolia* Spruce ex Warming stipulis incrassatis, foliis lanceolatis longe acuminatis, floribus calcari longo modice incurvo, petalo intermedio stamen aequante, stigmate terminali parvo instructis differt.

Holotypus: "coll. unknown" (comm. *D. Allen*) in U, fl. 14 Nov. 1953. PERU, Nanay River near Iquitos, altitude 100 m., "quillo sisa", tree more than 100 feet high, on clayey soil about 20 feet above river (Isotypes: US 2104976, Y 47782).

2. **Vochysia spathiphylla** Stafleu nov. spec. (fig. 1*c* and *d*).

Vochysia sectio *Ciliantha* Stafleu, subsectio *Ferrugineae* Warming. A. *V. lomatophylla* Standley petiolis crassioribus, laminis anguste spatulatis, subtus ferrugineo-tomentellis, supra praesertim ad nervos subsericeis, alabastris calcari magno valde recurvo instructis, filamento longiore, stylo stigmate terminali munito differt.

Arbor. Ramuli, petioli, stipulae, inflorescentia, foliorum pagina inferior indumento ferrugineo-canescente instructi, stipulae ovatae, acutae, c. 3–5 mm longae. Folia quaternata, petiolo c. 7–10 mm longo, 5–6 mm lato, lamina spatulata, c. 22–24 cm longa, c. 6–7 cm lata, apice rotundata, versus basin sensim in petiolum attenuata sed basi ipsa rotundata, supra praesertim ad nervos subsericea; nervis supra haud prominentibus, lateralibus subtus valde prominentibus, majoribus utrinque c. 20–25, sub angulo c. 60–80° e costa ortis a nervo limbali proxime marginem junctis, venulis supra haud conspicuis, subtus reticulatis. Inflorescentia densiflora, cincinnis 3–5-floris, pedunculis c. 12–15 mm longis, pedicellis c. 5–8 mm longis, alabastris ad 15 mm longis, haud recurvis, obtusis, calcari valde recurvo c. 14–18 mm longo, cylindrico, c. 3 mm lato instructis. Petala spatulata; intermedium c. 10–12 mm longum, dorso dense pilosum; lateralia modice breviora. Stamen intus pilosum, anthera c. 7 mm longa, filamento c. 3–4 mm longo; staminodia c. 1 mm longa, glabra. Stylus glaber, stigmate terminali parvo instructus.

Holotypus: Paul H. Allen 3248 in US; COLOMBIA, Vaupès, Cabeceras del Cubiyu, fl. 8 Dec. 1943. Tree, 12 m, flowers orange.

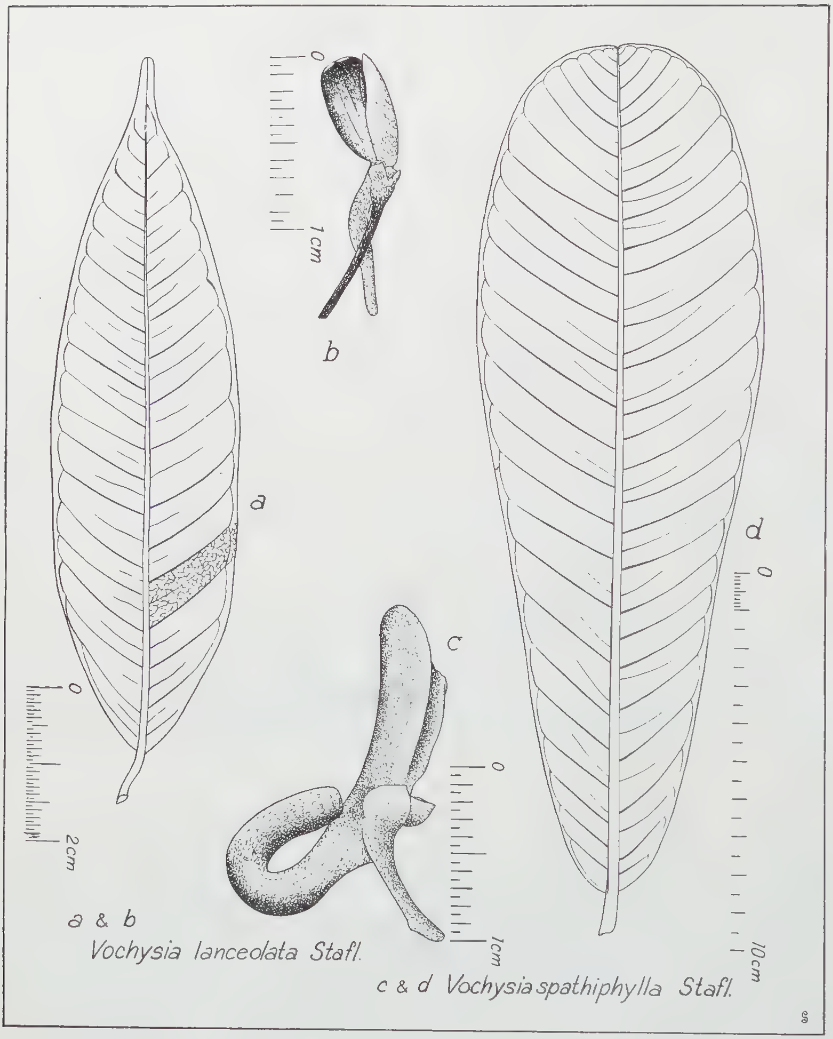
0
1cm
b
a
0
2cm
a & b
Vochysia lanceolata Stafl.
c
0
1cm
d
0
10cm
c & d Vochysia spathiphylla Stafl.

Fig. 1. *Vochysia lanceolata* Stafleu, *a.* leaf, *b.* flower; *Vochysia spathiphylla* Stafleu, *c.* flower, *d.* leaf.

3. **Vochysia artantha** Stafleu nov. spec. (fig. 2*a* and *b*).

Vochysia sectio *Ciliantha* Stafleu, subsectio *Ferrugineae* Warming, A. *V. calamana* Stafleu stipularum basibus linea prominula ramulum transiente connexis, foliis majoribus basi acutis, nervis lateralibus paucioribus in reticulum venularum excurrentibus, floribus petalo intermedio stamen aequante munitis differt.

Arbor satis magna. Ramuli juveniles, petioli, stipulae, folia juvenilia, ramuli inflorescentiae parce pilosi, demum glabrescentes. Stipulae triangulares, acuminatae, 1–2 mm longae, eae foliorum oppositorum basibus linea prominula ramulum transiente connexis. Folia opposita, petiolo c. 12–14 mm longo, lamina elliptica vel suboblanceolata, c. 10–12 cm longa, c. 3–4 cm lata, apice breviter obtuse acuminata, basi acuta, nervis supra haud prominentibus, lateralibus subtus prominentibus, utrinque c. 10, sub angulo c. 40–50° e costa ortis, prope marginem curvatis in reticulum venularum excurrentibus. Inflorescentia densiflora, cincinnis bifloris, pedunculis c. 3–4 mm longis, pedicellis c. 3–6 mm longis, alabastris ad 10 mm longis, parum recurvis, obtusis, calcari parum recurvo c. 6–7 mm longo, apice incrassato instructis. Petala subelliptica, intermedium stamen aequans, c. 7 mm longum, dorso parce pilosum, lateralia c. 4 mm longa. Stamen pilosum, anthera c. 6 mm longa, filamento c. 1 mm longo. Staminodia c. $\frac{1}{2}$ mm longa, ciliata. Stylus glaber, stigmate laterali c. 3/4 mm diam. instructus.

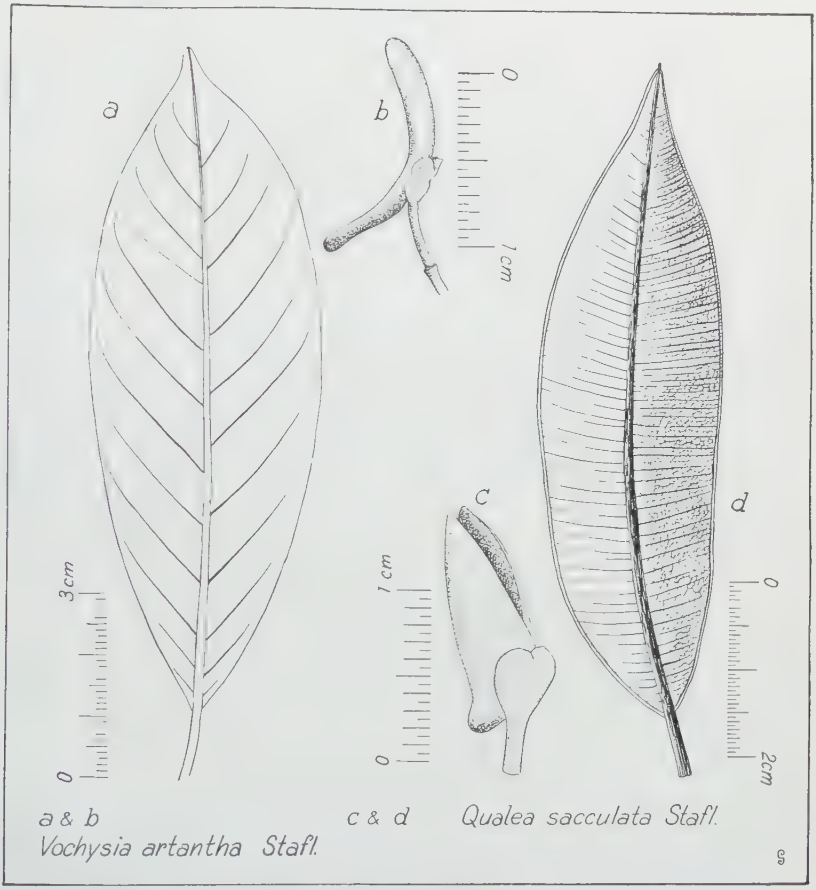

Fig. 2. *Vochysia artantha* Stafleu, *a*. leaf, *b*. flower; *Qualea sacculata* Stafleu, *c*. flower, *d*. leaf.

Holotypus: Paul H. Allen 3347 in US; COLOMBIA, Vaupès, vicinity of Mitu, fl. 21 March 1945. Trees averaging 30 m., "occurring as scattered colonies on slight prominences in otherwise nearly flat but unflooded forest".

4. **Qualea sacculata** Stafleu nov. spec. (fig. 2*c* and *d*).

Qualea subgenus *Qualea*, sectio *Trichanthera* Stafleu. A. *Q. rubiginosa* Stafleu glandulis semiglobosis, foliis longe petiolatis, acuminatis subtus persistenter tomentosis, alabastris fusiformibus, obtusis, floribus calcari sacculato, stylo glabro, ovario lanuginoso munitis differt.

Arbor. Ramuli juveniles, petioli, inflorescentia, foliorum pagina inferior indumento ferrugineo instructi. Glandulae semiglobosae, c. 1½ mm diam. Petioli c. 8–10 mm longi. Lamina rigide coriacea, lanceolata vel lanceolato-elliptica, c. 7–8 cm longa, c. 2–3 cm lata, apice acuminata, basi obtusa; nervis supra haud prominentibus, lateralibus subtus prominentibus, ultra 15 per cm, venulis numerosis. Inflorescentia pauciflora, cincinnis 1–2-floris (?), pedunculis et pedicellis haud visis, alabastris fusiformibus, obtusis, c. 11–13 mm longis, c. 3–4 mm latis, calcari sacculato, brevissimo, c. 1–2 mm longo instructis. Calycis laciniae minores subovatae, rotundatae, c. 2–3 mm longae, lacinia major c. 13 mm longa. Petalum glabrum, orbiculare, apice rotundatum. Anthera barbata, lineari-oblonga, acuta, c. 7 mm longa. Filamentum in alabastro c. 2 mm longum, expansum haud visum. Ovarium subconicum, dense lanuginosum, sensim in stylum transiens, indumento styli partem 1/6–1/10 inferiorem occupante.

Holotypus: H. García-Barriga 13828 in US; COLOMBIA, Vaupès, Rio Apaporis, entre los ríos Kananarí y Pacoa, alt. 250 m., fl. 1–15 Dec. 1951. "Arbol 15 m.; flores verde-amarillentas".

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SUBMICROSCOPIC STRUCTURE OF SOME CHLOROPLASTS

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(*received March 14th, 1957*)

INTRODUCTION

With regard to a study on chlorophyll concentrations in plastids from various species (THOMAS, MINNAERT and ELBERS (1956)) ultrathin sections of a number of these organelles were prepared and examined under the electron microscope. The technique used in this investigation is described in the present paper while some of the electron micrographs are shown and discussed.

METHODS

Freshly collected leaves were cut into pieces of about 0.5 mm thickness. Unicellular algae and bacteria were harvested by centrifugation.

Fixation was carried out in a 1 % osmium tetroxide solution, phosphate-buffered at p_H 7.2. The specimens were fixed at room temperature for 4 hours. Afterwards, they were briefly washed with distilled water, transferred into 70 % ethanol and left there overnight. After dehydration with 96 % ethanol for 2 hours and, next, with freshly prepared 100 % ethanol for 3 hours -3 changes- the specimens were transferred into a mixture of 90 % n-butyl- and 10 % methylmethacrylate containing 1 % Luperco CDB (2, 4 dichlorobenzoylperoxide) as a catalyzer. During the following 3 hours the methacrylate was changed twice. Next, the specimens were embedded in a pre-polymerised methacrylate mixture. Complete polymerisation was obtained at 45° C after 36 hours.

Cutting was done with the aid of a glass edge. The microtome we used was constructed according to the following design, *cf.* Fig. 1.

The specimen block is radially inserted in a steel cylinder (1) with a diameter of 4.5 cm and rotating with a specially devised axis in a V-shaped bearing (2). The axis was ground, lapped and honed to the highest possible degree of roundness.

The knife is adjusted in its holder between two rigid spring blades

(3) which are vertically mounted on a support with micrometer screw for gross adjustment. The top ends of the springs together with the knife holder move towards the rotating specimen by thermal expansion of a small brass bar (4) which is mounted between the knife holder support and a rigid stop block. This brass bar is heat-insulated from the microtome by means of two glass beads. It is heated electrically from room temperature to about 60° C. This meets the preparation of 2500 sections of 200 Å thickness.

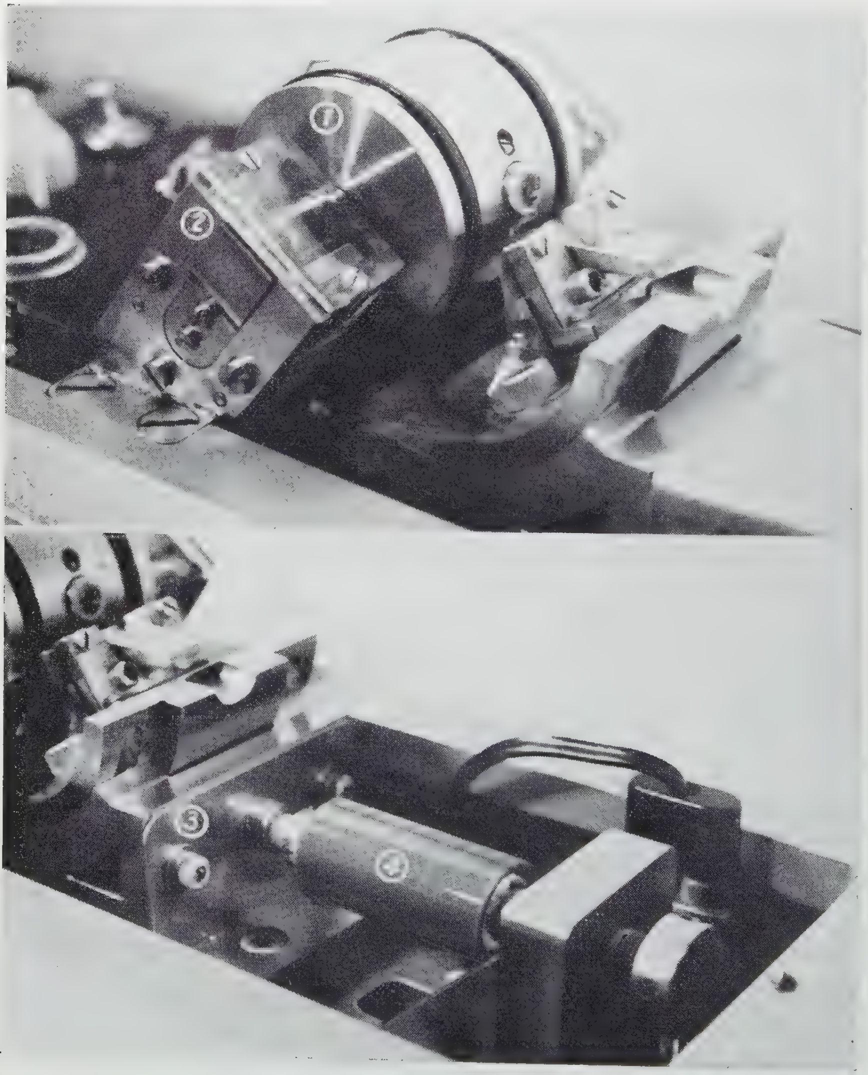
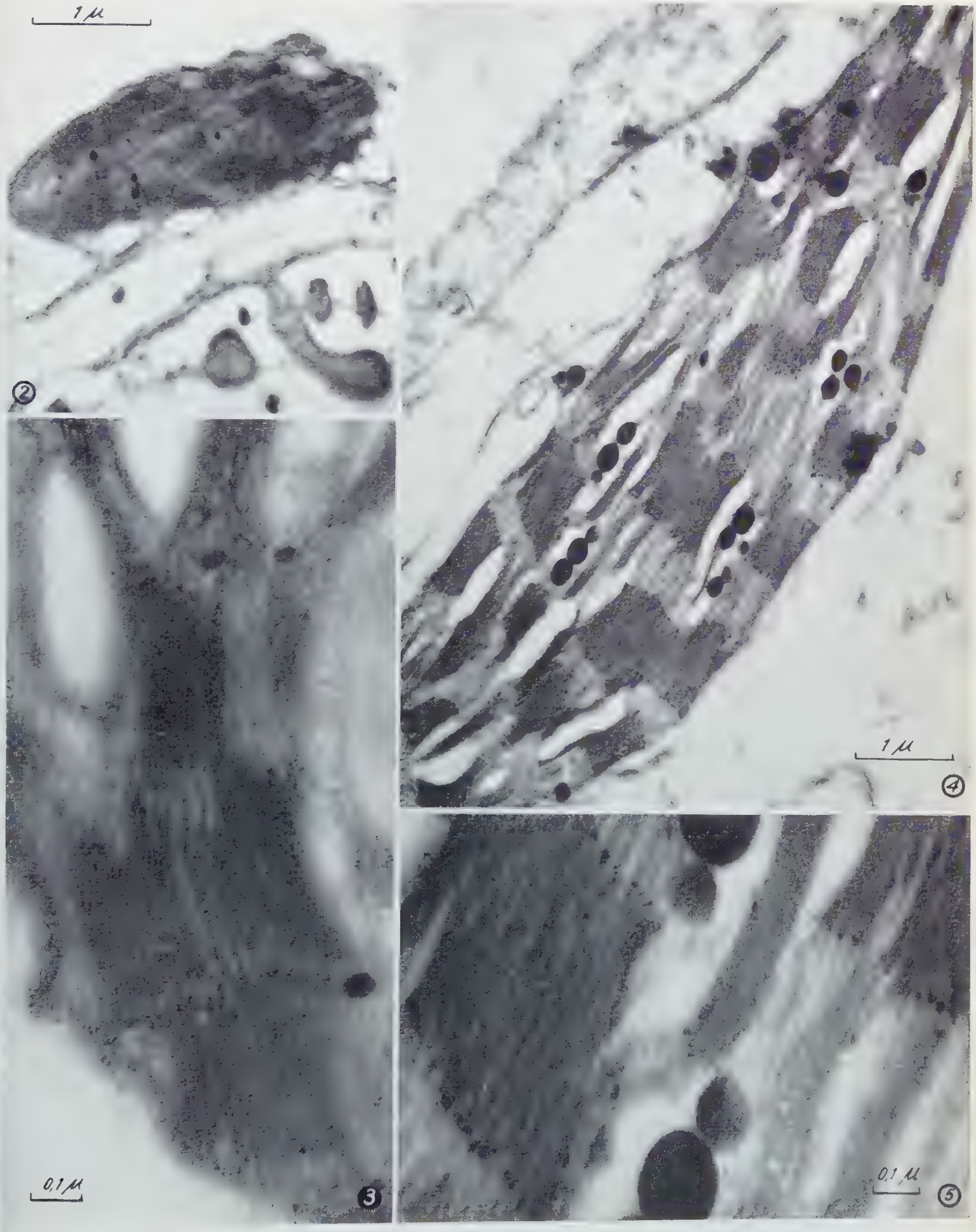
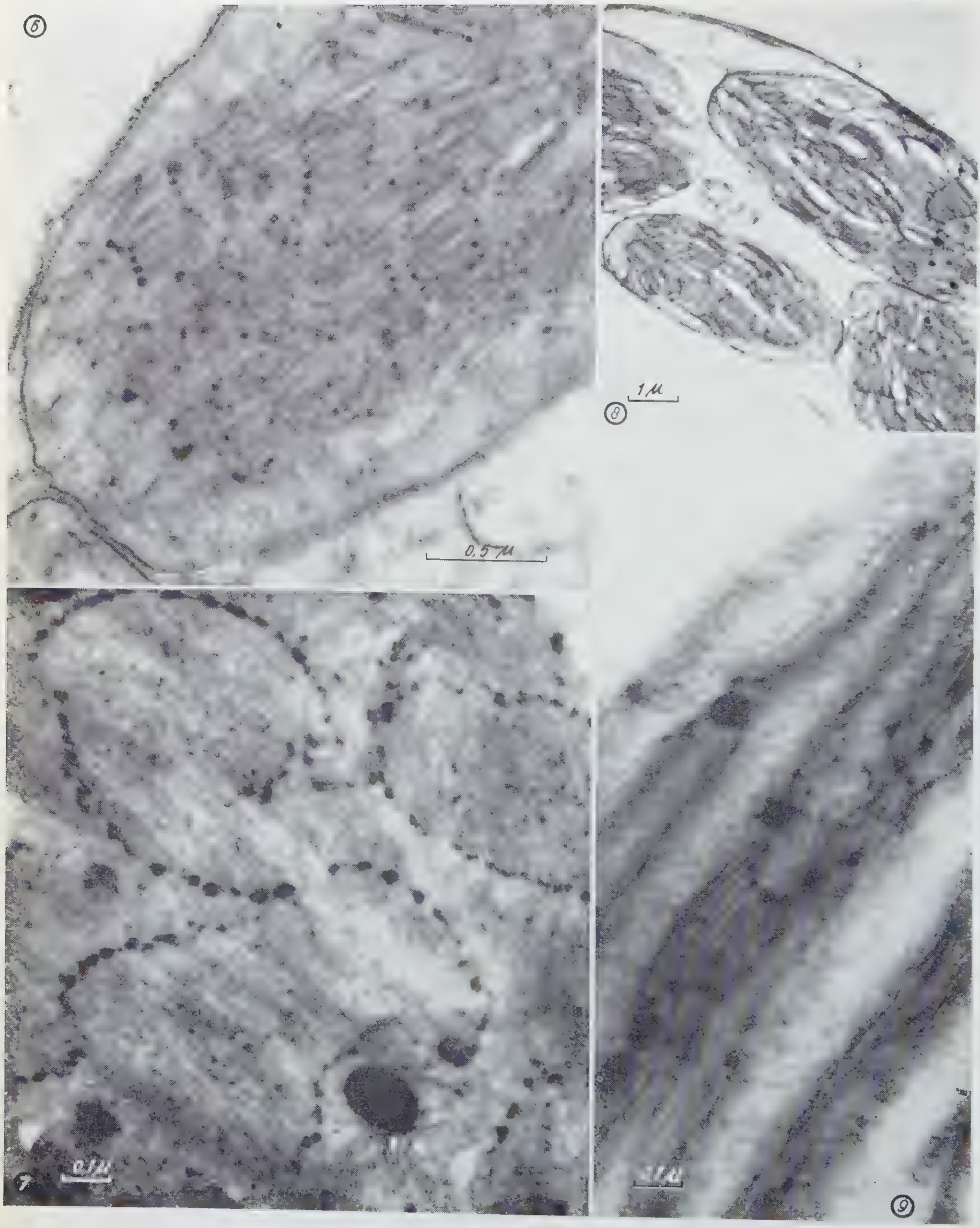


Fig. 1. The microtome. Explanation see text.

PLATE I

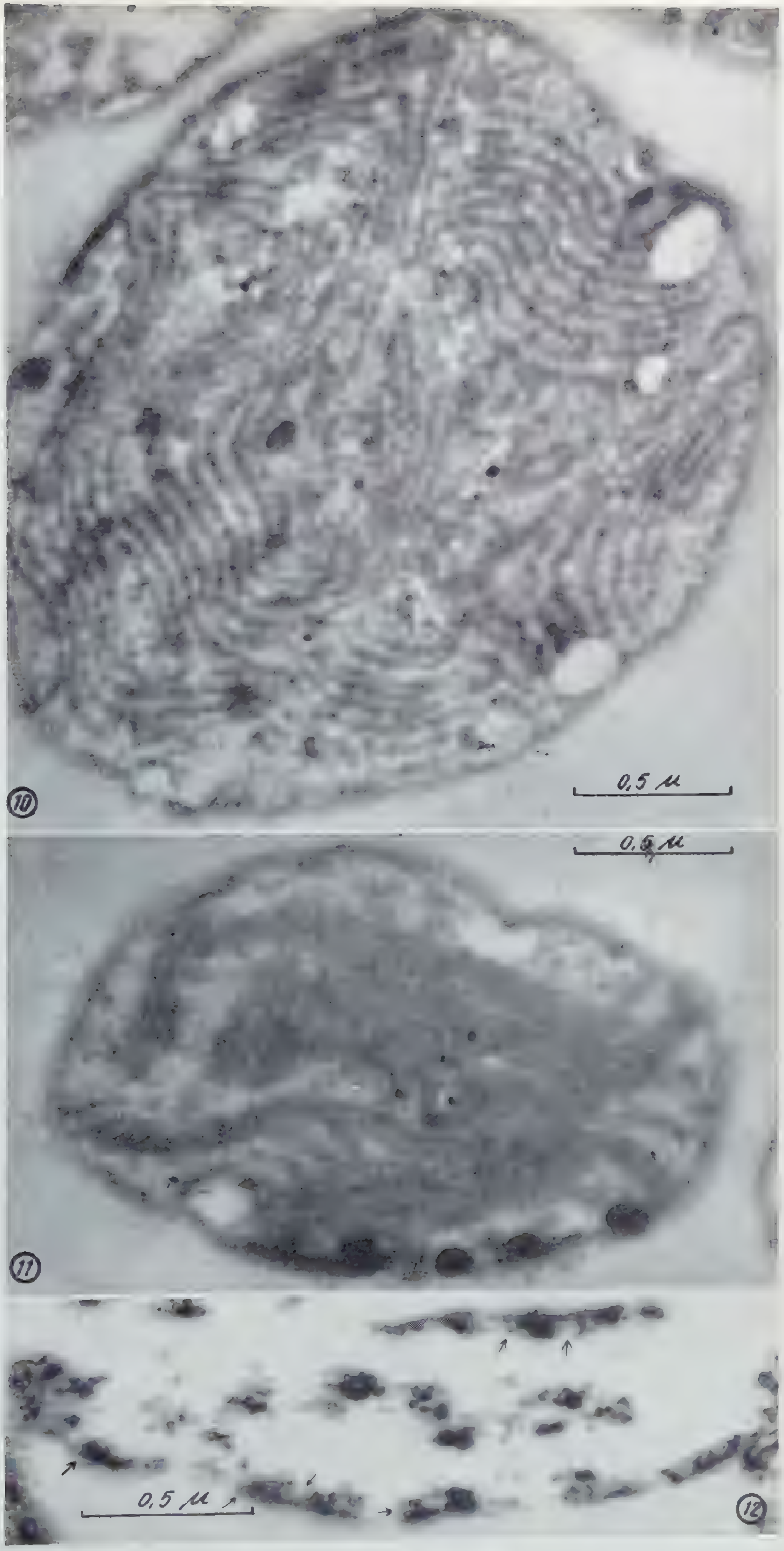


Figs. 2–5. 2: Chloroplast of *Elodea densa*. 3: Detail of fig. 2. 4: Chloroplast of *Aspidistra elatior*. 5: Detail of fig. 4.



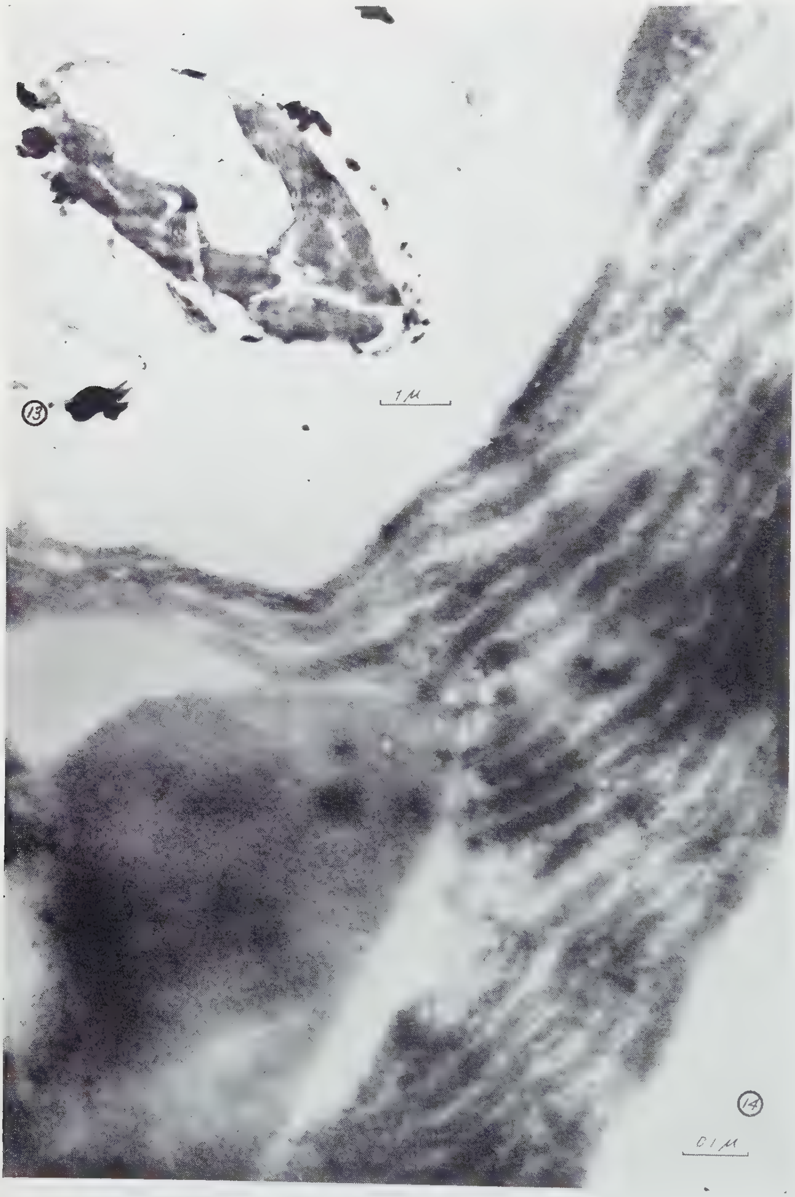
Figs. 6–9. 6: Tulip chloroplast. 7: Detail of a chloroplast of *Hibiscus rosa sinensis*. 8: Chloroplasts of *Hibiscus rosa sinensis*. 9: Chloroplast of the sugar beet.

PLATE III



Figs. 10–12. 10 and 11: Sections of whole cells of *Synechococcus cedrorum*. 12: Section of a cell of *Rhodospirillum rubrum*.

PLATE IV



Figs. 13–14. 13: Section of a whole cell of *Nitzschia dissipata*. 14: Detail of the chloroplast from fig. 13.

The heating current can be controled with a potentiometer and a transformer. A section thickness of 200 Å is obtained with a heating current of 80 mA at 4.5 V. The steel cylinder carrying the specimen is rotated by a vibration-free coupled asynchronous electromotor with a high torque providing a cutting period of about one second.

The actual cutting speed is regulated as follows. The rotating steel cylinder operates an electronic relay which reverses the electric connections to the motor when the specimen reaches a point at about 60° before the cutting position is reached. This yields a turning force in the opposite direction for the motor. The braking effect thus obtained is regulated with a variable resistance in the proper electric connections to the motor. Just after cutting, the electric connections are reversed again by the electronic relay, thus allowing the steel cylinder to rotate once more at the original speed.

In this way a very low actual cutting speed can be obtained, the cutting period remaining short and practically constant. Such a low cutting speed is essential for avoiding vibrations of the block and the knife edge during the cutting of the object.

The microtome has now worked satisfactorily for a period of $2\frac{1}{2}$ years.

The sections were studied with a Philips microscope type EM 100 at 60 kV. The minimum astigmatism of the 25 Å non-compensated objective lens was about 1.5 μ. The photographs were made at initial magnifications of 2700 ×, 6500 ×, and 13000 × on Kodak Fine Grain Positive film and processed in Kodak D 11 or D 19 b developer. The prints were made on extra hard paper.

Results

Fig. 2 represents a section of a chloroplast of *Elodea densa*. Between the grana, stroma lamellae are visible. The stroma, however, also consists of a granular component. Some details are shown in Fig. 3. The stroma lamellae seem to show a forking as they enter the grana. In this way double lamellae are formed. At the boundary of the grana osmiophilic substance is present. The same is shown most clearly in sections of chloroplasts of *Aspidistra elatior*, *cf.* Figs. 4 and 5, tulip, Fig. 6, and *Hibiscus rosa sinensis*, Figs. 7 and 8. Apart from these osmiophilic regions at the granum-stroma boundary, relatively large osmiophilic globules occur in the stroma. They can be seen very clearly in Figs. 4 and 5.

The sections mentioned so far were prepared from full-grown chloroplasts. It is obvious that the ratio of the quantities of both lamellar and granular stroma varies for chloroplasts from various species.

Fig. 9 shows developing grana in a young chloroplast of *Beta saccharifera*. At the lamellar furcation points concentration of osmiophilic substance is discernable.

Figs. 10 and 11 represent sections of the blue-green alga *Synechococcus cedrorum*. Instead of free grana, as was anticipated, a more or less cup-shaped chloroplast can be observed in Fig. 11. Most probably, Fig. 10 shows a cross-section through the "bottom" of the chloroplast "cup". This figure also shows that the lamellae occur in bundles.

Fig. 12 shows free grana in the purple bacterium *Rhodospirillum rubrum*. The spots at which lamellae are discernable are indicated by arrows.

Figs. 13 and 14 refer to a chloroplast of the diatom *Nitzschia dissipata* containing a large deposit of photosynthesates (×). The lamellae occur in bundles of 4 to 6 throughout the chloroplast.

DISCUSSION

Since, due to the presence of lipids, in dried chloroplast preparations precipitation membranes were observed under the electron microscope, it was argued by *e.g.* FREY–WYSSLING and STEINMANN (1953) that layers which were interpreted to represent chloroplast membranes may well be such precipitation membranes. Though this possibility should not be neglected, results obtained with improved sectioning techniques seem to prove that chloroplast membranes do occur. This evidence was procured by LEYON (1954) who also noticed that this membrane consists of two layers, and by MERCER *et al.* (1955) who, moreover, found indications for the view that the chloroplast membrane is differentially permeable. The present electron micrographs, Figs. 2, 4, 6, and 8, support the evidence for the existence of an outer chloroplast membrane. At × in Fig. 6 an indication of its two-layered structure occurs.

Electron micrographs of dried chloroplast suspensions suggest that grana are disc-like structures. From experiments on mild protease and lipase digestion of spinach grana THOMAS, BUSTRAAN and PARIS (1952) concluded that, most probably, these grana are surrounded by a membrane consisting of an inner protein layer and an outer lipid one. However, in electron micrographs of ultra-thin sections grana membranes were not observed and, thus, the membrane-like structures described by these authors may well be artifacts. Moreover, the sectioning technique reveals that the way in which the intragranar lamellae are piled up is not as perfect as is suggested by pictures of dried grana suspensions.

What happens to stroma lamellae as they enter grana, is a question on which opinions diverge. LEYON (1954, 1956) suggested that, in the *Aspidistra* chloroplast, "some substances" are deposited at distinct circular spots of the stroma lamellae which become thickened in this way. A pile of such thickened lamellae may constitute a granum. Thus, the number of grana lamellae is the same as that of stroma lamellae. However, LEYON mentioned that, in the micrographs, the boundary between grana and stroma lamellae often is somewhat obscured because of the occurrence of osmiophilic substance in this region. The occurrence of such a substance was also observed in the present study.

HODGE, MCLEAN and MERCER (1955), working with chloroplasts of *Zea mays* and *Hydrangea*, observed a forking of the stroma lamellae as they enter the grana. In this way, the number of grana lamellae is twice that of stroma lamellae.

STEINMANN and SJÖSTRAND (1955) presented a schematic picture of *Aspidistra* grana in which they agreed with LEYON with regard to the ratio of both kinds of lamellae. However, they assumed that LEYON's "deposited substance", apart from covering the opposite surfaces of a pair of lamellae, also connects these layers at the peripheral zone of the granum. In this way, a granum lamella was suggested to consist of two layers which are linked together at the periphery of the granum. Fine electron micrographs support this conception. However, these pictures do not seem to exclude the possibility that forking of the lamellae, when entering the grana, also occur in *Aspidistra* chloroplasts at some spots.

STUBBE and VON WETTSTEIN (1955) presented a schematic picture for *Oenothera* chloroplasts, which, in a sense, is intermediary between those of LEYON (1956) and STEINMANN and SJÖSTRAND (1955).

As far as can be concluded from the present micrographs, both forking of stroma lamellae when entering the grana, and a linking in pairs of these lamellae by the aid of "some substance" in this region, might occur in chloroplasts of *Elodea*, *Aspidistra*, tulip and sugar beet. However, to the authors' opinion some uncertainty about this conception remains. In any case, the grana lamellae of *Aspidistra* must consist of two circular layers which are connected to each other at their circumference. Otherwise, swelling phenomena such as those obtained by FREY–WYSSLING and STEINMANN (1953), see their Figs. 10 and 11, could never occur.

In contrast with the widely accepted conception, no free grana were observed in the blue-green alga *Synechococcus cedrorum*. When an aqueous extract of this alga is studied under the electron microscope, grana-like structures are observed (CALVIN and LYNCH, (1952), THOMAS (1952)). Apparently, these structures are artifacts. Fig. 11 shows the occurrence of a cup-shaped chloroplast in which the lamellae occur in bundles of 4–6 throughout the plastid. This chloroplast more or less resembles the *Chlorella* chloroplast (ALBERTSSON and LEYON, (1954)). In *Phormidium uncinatum*, also a blue-green alga, NIKLOWITZ and DREWS (1955*a*) observed a lamellate "Chromatoplasma". At distinct spots the lamellae are thickened in a grana-like manner. The authors are of opinion that here too a single "chromatophor" per cell occurs.

NIKLOWITZ and DREWS (1955*b*) also prepared ultra-thin sections of the Athiorhodacea *Rhodospirillum rubrum*. The present Fig. 12 is in agreement with their results.

The structure of the diatom chloroplast, Figs. 13 and 14, much resembles that of the *Fucus* chloroplast (LEYON and VON WETTSTEIN, (1954)). This figure may demonstrate that the chlorophyll-bearing plastid of the diatom *Nitzschia dissipata*, *cf.* THOMAS, MINNAERT and ELBERS (1956), should be considered as a lamellate chloroplast. The lamellae occur in bundles of 4–6 also here.

SUMMARY

A microtome for preparing ultra-thin sections is described.

Some electron micrographs of chloroplasts from different species and of free grana in a purple bacterium are presented and discussed.

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ON THE POSITION OF PLATYCARPUM HUMB. ET BONPL., HENRIQUEZIA SPRUCE EX BTH. AND GLEASONIA STANDL.

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(*received February 15th, 1957*)

INTRODUCTION

Some time ago the "Instituto Agronómico do Norte, Belem, Pará, Brazil" sent me a set of specimens for identification among which I detected a new species of *Henriquezia* Spruce ex Bth. This discovery induced me to study once more and now in somewhat more detail the relation between this genus and the nearly related *Platycarpum* Humb. et Bonpl. and the position these two genera occupy with regard to the habitually rather similar *Gleasonia* Standl., a subject to which I had already paid some attention at an earlier occasion, and on which I had reported in a note which is to be found at the base of p. 16 of my work on "the African Species of Oldenlandia L sensu Hiern et K. Schumann" in Verh. Kon. Ned. Akad. v. Wetensch., Sect. 2, 48, no 4, 1952. By the good office of Dr Bassett Maguire I received on loan from the New York Botanical Garden the rich materials by which, as a result of the Botanical Garden's recent expeditions to Tropical America, these genera are represented in its herbarium, and during a recent visit to England I could study also the valuable collections in the herbarium of the Royal Botanic Gardens, Kew. In the course of these studies I discovered among the *Platycarpum* specimens too a new species. Descriptions of the latter and of my new *Henriquezia* will be found further on in this paper. They are, however, but of secondary importance; the main object of this study is to ascertain as precisely as possible the taxonomical position of these three rather puzzling genera.

In the note on p. 16 of my work on "the African Species of Oldenlandia L sensu Hiern et K. Schumann" I stated that *Gleasonia* Standl. "on account of the large and flat exalbuminous seeds and also because of the very peculiar structure of the testa is to be referred to the *Henriquezieae*, a tribe that will have to be removed as a separate family to the *Tubiflorae*." In support of this opinion I referred to Fig. c, d, e and f of Tab. V, which represent the testa of *Henriquezia verticillata* Spruce ex Bth., of *Platycarpum orinocense* Humb. et Bonpl. and of two species of *Gleasonia*, viz. *Gl. uaupensis* Ducke and *Gl. macrocalyx* Ducke.

The study of the more abundant and better material that I had now at my disposition has led to a somewhat different standpoint. The differences between *Gleasonia* and the two other genera appeared to be of far greater taxonomical importance than the points of resemblance, and although this more detailed study did not shake the opinion I had arrived at with regard to the genera *Platycarpum* and *Henriquezia*, viz. that they are to be regarded as representatives of a new family *Henriqueziaceae*, for which on account of its affinity with the *Bignoniaceae*, *Pedaliaceae*, *Martyniaceae*, *Thunbergiaceae*, *Mendonciaceae* and *Acanthaceae*, a position will have to be found in the order *Tubiflorae*, I now see that the genus *Gleasonia* can not be regarded as a very near ally, and that it is either to be left in the *Rubiaceae*, where it occupies, on account of the exalbuminous seeds and the large size of the cotyledons, an anomalous position, or else to be referred to a new family, which however, on account of the structure of flower and fruit and of the presence of colleters on the inside of the stipules, would have to be placed in the near vicinity of the *Rubiaceae*. This implies, of course, that the points of resemblance between *Gleasonia* and the genera *Platycarpum* and *Henriquezia*, on which I based my former view, are no longer accepted by me as homologies, but that I now regard them as mere analogies.

The change in my opinion with regard to the taxonomical position of *Gleasonia* is due to a better insight in the characters in which this genus differs from the two other ones and in those in which it resembles them. In order to facilitate a discussion, I will first of all give an enumeration of the differences, as the latter are in this respect of more importance than the points of resemblance.

Comparison between *Gleasonia* and the genera *Platycarpum* and *Henriquezia*.

The principal differences between *Gleasonia* and the two other genera are: 1) the absence in *Gleosonia* of the peculiar "glands" that in *Platycarpum* and *Henriquezia* are found at the base of the petiole, and which in fact are found nowhere else in the whole kingdom of plants; 2) the presence of colleters or resin glands on the inside of the stipules of *Gleasonia*, a character which this genus shares with the great majority of the *Rubiaceae*, and their absence in *Platycarpum* and *Henriquezia*; 3) a different structure of the corolla, that of *Gleasonia* being actinomorphous with induplicate aestivation of the lobes, that of the two other genera zygomorphous with a longitudinal streak of hairs on the ventral side of the throat and with ascending aestivation (cf. Fig. 1); 4) a different structure of the androecium, which

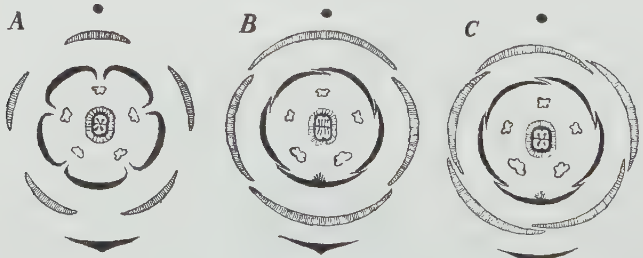

Fig. 1. Floral diagrams of A. *Gleasonia duidana*, B. *Henriquezia verticillata* and C. *Platycarpum orinocense*.

in *Gleasonia* is subregular, in *Platycarpum* and *Henriquezia* distinctly zygomorphous, the filaments being inserted at unequal height, bent at the base and of unequal length; 5) a different arrangement of the ovules (cf. Fig. 2), those of *Gleasonia* forming in each ovary cell a double row which ascends to about midway the dissepiment, whereas the two to four ovules found in each of the ovary cells of the two other genera are inserted at nearly the same height; and 6) a different development of the capsule, that of *Gleasonia* (Fig. 9, p. 000) remaining entirely inferior, whereas that of the two other genera becomes either semi-superior (*Henriquezia*, Fig. 11, p. 000) or even almost completely superior (*Platycarpum*, Fig. 10, p. 000). Less important points of difference are found in the arrangement of the pollen grains, those of *Gleasonia* (Fig. 3) remaining united in tetrads, whereas they are set free in the two other genera, and also in their structure, those of *Gleasonia* always being 3-colpate, those of the other genera (Fig. 4) either 3- or 4- or 5- or 6-colpate, in the number and shape of the seeds, those of *Gleasonia* being more numerous and more or less swollen and angular, whereas the two to four seeds of the two other genera are flat, and in the structure of the testa, the cells being convex in *Gleasonia*, and produced into papillae in *Henriquezia* (Fig. 5) and *Platycarpum* (Fig. 6). Before proceeding to the points of resemblance, it will be well to discuss these differences, the more important ones as well as the others, in some detail.

The "glands" which in *Platycarpum* and *Henriquezia* are seen at the base of the petiole on the side facing outwards, are large glabrous and shiny spots slightly protruding beyond the surrounding tissue; in herbarium material they at once draw the attention by the black colour they assume in drying. Their exact nature is unknown: it is possible that they secrete a sugary fluid, and in that case they would belong to the large class of extra-floral nectaries, but it may also be that they are bacterial nodules; without living material it will probably be difficult to settle this point. Howsoever this may be, these petiolar "glands" certainly are a very characteristic feature of these two genera, the like of which is found nowhere else.

The presence of colleters or resin glands on the inside of the stipules of *Gleasonia* is a character which this genus shares with the majority of the *Rubiaceae*. In fact, they are, as was shown by Krause (Ueber harzsecernierende Drüsen an den Nebenblättern von Rubiaceen, in Ber. d. d. bot. Gesellsch. 27: 446–452. 1909), found in all tribes of this family with the exception of the *Rubieae* (*Galieae*). Their absence in this tribe might be an argument in favour of the view that the supernumerary leaf-like parts of these plants are no modified stipules, as is now commonly accepted, but that they are true leaves.

According to Krause colleters would be present in the genus *Henriquezia* too, but this must be a mistake. Although I did not investigate the species quoted by him, the apparently very rare *H. nitida* Spruce ex Bth., I studied three other species, viz. *H. verticillata* Spruce ex Bth., *H. macrophylla* Ducke and *H. longisepala* Brem. v. infra, and in addition several species of *Platycarpum*, but in none of them I could find the slightest trace of these structures. I suppose therefore that the specimen studied by Krause will have been misidentified, and that it belonged in reality to some other genus.

It is noteworthy that although colleters are by no means confined to the *Rubiaceae* (cf. HANSTEIN in Bot. Ztg 26: 697–713, 720–735, 744–761 and 768–787. 1868), they are in this family of a rather peculiar structure which returns only in the *Cunoniaceae*, a family that may be distantly related to the *Rubiaceae*, and in the genus *Viola*. That the colleters of *Gleasonia* too are of this type, is certainly a weighty argument in favour of the view that this genus belongs either to the *Rubiaceae* themselves or else to a new family for which a place will have to be found in the near vicinity of the latter.

That the corolla of *Gleasonia* is actinomorphous is in itself perhaps not very important, but in connection with the valvate, or more precisely induplicate, aestivation of its lobes it is certainly not easily reconcilable with the view that this genus would be a near ally of *Platycarpum* and *Henriquezia*, where the corolla is more or less distinctly zygomorphous with a longitudinal strip of hairs on the ventral side of the throat, and where the aestivation is ascending-imbricate.

The zygomorphism of the corolla would not exclude the genera *Platycarpum* and *Henriquezia* from the *Rubiaceae*, for slightly zygomorphous corollae are in this family certainly not unknown, although they never show a band of hairs on the ventral side of the throat. A slightly unequal length of the filaments is here, as an accompanying feature, not uncommon either. As examples of such a slight zygomorphism of the androecium corresponding to a curvature of the upper part of the corolla, we may refer to the genera *Pallasia* Klotzsch, *Macrocnemum* Wedd., *Ferdinandusa* Pohl and *Posoqueria* Aubl. This form of zygomorphism, however, is of little importance as it does not obscure the fundamental symmetry of the plan according to which the flower is built. In this respect it is of hardly more value than the zygomorphism of the calyx that is so often met with in genera belonging to this family, and which is due to the development of one of the calyx lobes into a foliaceous appendage, a form of zygomorphism that does not affect the other parts of the flower, and is moreover restricted to a few flowers per inflorescence. The androecium of *Platycarpum* and *Henriquezia*, however, shows a fundamentally different form of zygomorphism, which finds its expression in the insertion of the filaments at unequal height and in a curvature of their basal part. Among the genera for which a position in the *Rubiaceae* has been claimed, the number of those that are provided with a zygomorphous androecium of this kind is very small indeed, and there is in all these instances (e.g. *Tammsia* Karst., *Aitchisonia* Hemsl.) good reason to doubt the correctness of their classification; in none of them, moreover, the filaments are bent at their base.

The difference in the arrangement of the ovules is another argument against the view that *Gleasonia* would be a near ally of *Platycarpum* and *Henriquezia* (cf. Fig. 2), but the arrangement itself gives us no indication with regard to the taxonomic position either of *Gleasonia* or of the two other genera, for arrangements similar to that seen in *Gleasonia* as well as arrangements of the kind observed in *Platycarpum* and *Henriquezia* are found in families belonging to very different families and orders.

The capsule of *Gleasonia* (Fig. 9, p. 364) is of a type for which we might easily find a place within the range of those that are met with among the *Rubiaceae*, but the semi-superior or almost completely superior capsules found in *Henriquezia* (Fig. 11, p. 373) and *Platycarpum* (Fig. 10, p. 372) are of a more aberrant kind. Nevertheless their deviation from the ordinary inferior type of capsule, although accentuating once more the width of the gap which separates these two genera from *Gleasonia*, would in itself not be sufficient to exclude these genera from the *Rubiaceae*, as a similar deviation occurs in the tribe *Gaertnerieae*, whose position in the family must, on account of its very close resemblance to the *Psychotrieae*, be regarded as well-established.

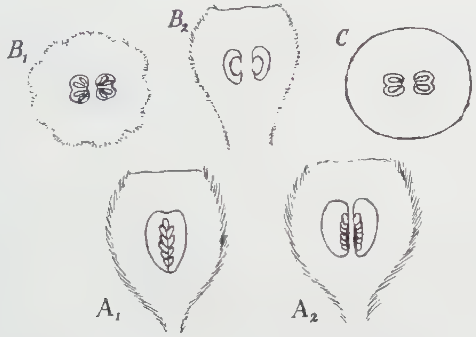

Fig. 2. Ovary of A. *Gleasonia duidana*, B. *Henriquezia longisepala*, and C. *Platycarpum orinocence*. Note the ridge opposite the placenta in the ovary cells of *Henriquezia* and *Platycarpum*.

The less important differences mentioned at the end of our list, are found in the pollen characters and in number, shape and structure of the seeds.

That the pollen grains of *Gleasonia* (Fig. 3) remain united in tetrads, is doubtless a somewhat unexpected feature, which sharply differentiates this genus from *Platycarpum* and *Henriquezia*, but whose taxonomical importance should not be overrated. It is certainly not a character on account of which the genus would have to be excluded from the *Rubiaceae*, for pollen grains united in tetrads are not unknown in this family; they are e.g. a general character of the genus *Randia* (Houst.) L sensu Fagerlind. The uncommonly large size of the individual grains (diam. 70 μ in *Gl.uaupensis* and 110 μ in *Gl.duidana*) is in this respect perhaps of somewhat greater importance, as the pollen grains of the *Rubiaceae* are, on the whole, rather small; even the largest ones that are known so far (they were found in the genera *Richardia* (Houst.) L. and *Palicourea* Aubl.) are not so bulky as those of *Gleasonia*. That the pollen grains of *Platycarpum* and *Henriquezia* too are very large, is, of course, a point of resemblance between these

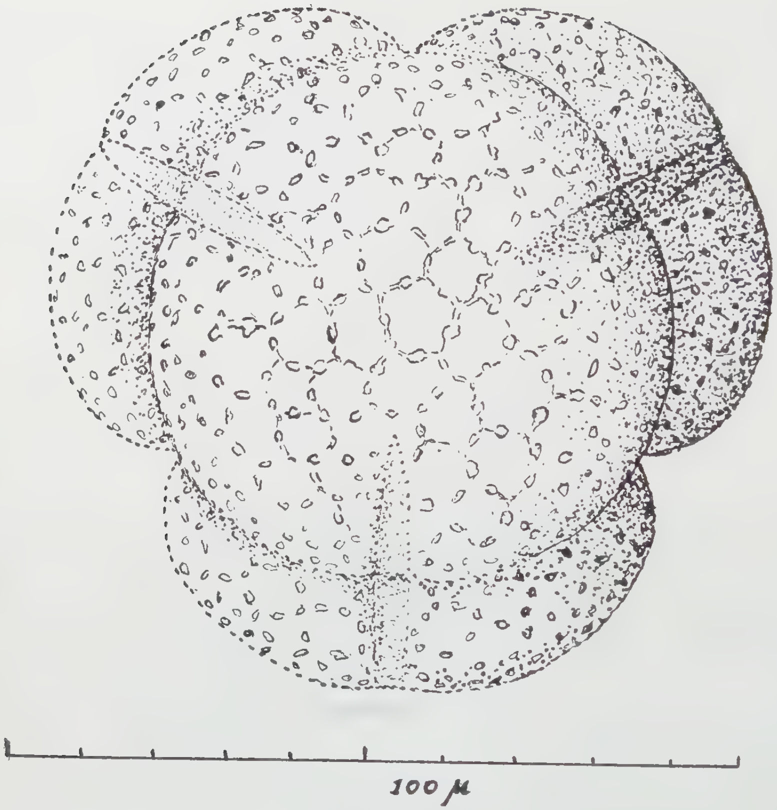

Fig. 3. Pollen tetrad of *Gleasonia uaupensis.*

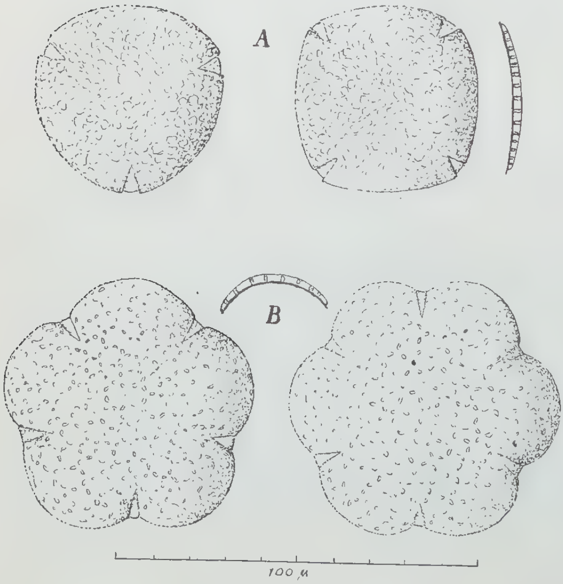

Fig. 4. Pollen grains of A. *Platycarpum orinocense,* and B. *Henriquezia macrophylla.* The figure to the right of A and that between the two pollen grains of B are optical sections of the wall.

genera and *Gleasonia*, but not one of any importance, as large pollen grains are met with in very different circles of affinity. That the pollen grains of *Platycarpum* and *Henriquezia* (Fig. 4) are usually provided with more than three colpae, is on the other hand worth noting, not only because it constitutes a difference with *Gleasonia*, but also because pollen grains with more than three colpae (or pores) usually characterize groups of a rank far exceeding that of the genus. It is also noteworthy that pollen grains of a very similar type are met with in several of the families of the *Tubiflorae* with which the genera *Platycarpum* and *Henriquezia* show points of resemblance (*Bignoniaceae*, *Pedaliaceae*, *Mendonciaceae*, see on the pollen structures met with in these families my paper on "The Position of the genus *Thomandersia* Baill." in Rec. d. trav. bot. neerl. 39: 166–175. 1942).

The differences in number and shape of the seeds are not very important either and moreover somewhat obscured by the very striking points of resemblance, viz. the absence of endosperm and the strong development of the cotyledons, points that we will discuss hereafter. The seeds of *Gleasonia* are more numerous than those of the two other genera, where each of the fruit cells contains but one to four seeds, and they are angular and less strongly compressed.

The difference in the structure of the testa is doubtless of greater importance. The testa cells of *Platycarpum* (Fig. 5) and *Henriquezia* (Fig. 6) are drawn out into papillae or short hairs; those of *Gleasonia* are merely convex. The presence of papillae on the testa was known so far only for *Platycarpum*, but a renewed study of the testa of *Henriquezia verticillata* Spruce ex Bth. has led to the conclusion that they are present in this genus too. That they were originally overlooked was due to the circumstance that the seed investigated at that time

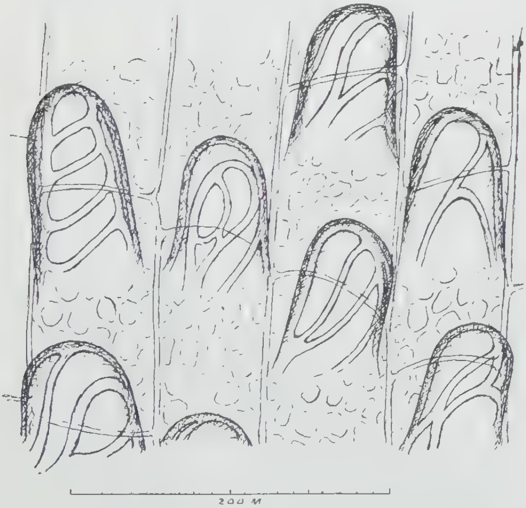

Fig. 5. Testa of *Platycarpum orinocense*.

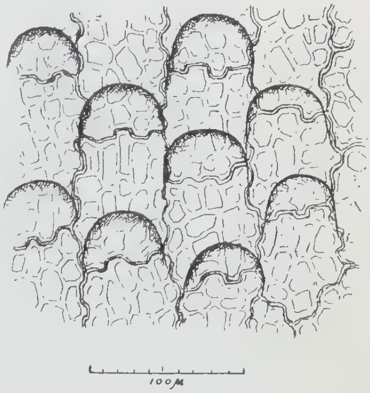

Fig. 6. Testa of *Henriquezia verticillata*.

was fully mature; at that stage the outer wall of the testa cells has disappeared; the wall shown in my original figure is the reticulate inner one. For this reason I insert here a new figure in which the outer wall with the papillae is shown. An exactly corresponding structure of the testa is met nowhere in the *Rubiaceae*, but this would in itself not be enough to exclude these genera, as the variability in the structure of the testa is so large in this family that it is as yet impossible to decide what would fall outside its range.

In the genus *Gleasonia* the structure of the testa proves to be of an entirely different kind. The two figures given in my earlier communication are unsatisfactory, as the seed of *Gl. uaupensis* Ducke of which I studied the testa, was not yet fully mature, and as that of *Gl. macrocalyx* Ducke was so young that the sclerization of the outer wall had not yet begun. Ripe seeds of *Gl. macrocalyx* were this time too not available, so that I am still unable to tell in how far the structure of their testa agrees with that seen in the two other species. The wartlets on the testa, of which one was figured in my earlier publication, are at any rate a feature by which these seeds differ from those of the two other species. Of the latter, *Gl. duidana* Standl., the species on which the genus was founded, and *Gl. uaupensis*, fully mature seeds could now be studied. The testa cells of these two species have a convex outer wall, which proves to be provided with an irregular network of thickenings (Fig. 7), which in fully mature seeds extends over the lateral walls too. The nearest approach to this structure is found in *Hillia* Jacq., a genus which occupies a rather isolated position in the family, but which, i.a. on account of the presence of raphides, can certainly not be regarded as a near ally (see for this genus my work on "the African Species of Oldenlandia L sensu Hiern et K. Schumann" p. 14 and 15 and Tab. V fig. a); the cells of the *Hillia* testa, however, are of a different shape, and their lateral

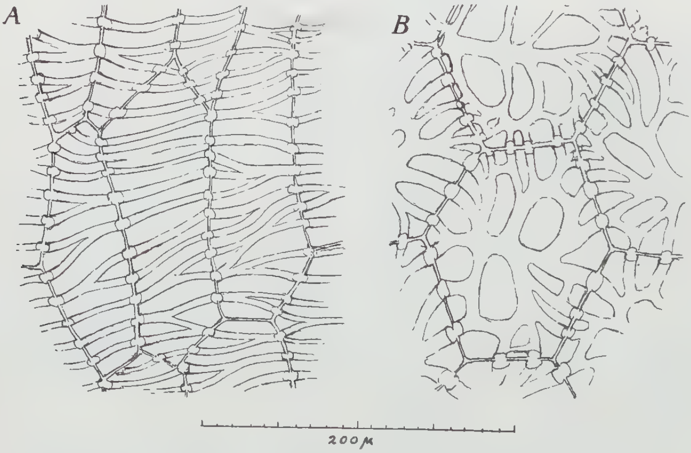

Fig. 7. Testa of A. *Gleasonia duidana*, and B. *Gl. uaupensis*.

walls are much thicker. The structure of the testa cells shows that the genus *Gleasonia*, if it is to be included in the *Rubiaceae*, will have to be referred to a tribe or even to a subfamily of its own, and that it certainly can not be put in the *Rondeletieae*, as was done by Standley. In this tribe the basal wall of the testa cells is provided with very large round or oval pits, which means that it shows the structure which is characteristic for the subfamily to which this tribe belongs, viz. the *Cinchonoideae* sensu meo (see my paper on the subdivision of the family in "Rapports et Communications aux Sections 2, 4, 5 et 6, Huitième Congrès de Botanique: 113, 1954), and these large pits are in *Gleasonia* completely absent.

Now that we have finished our discussion of the indications the differences between *Gleasonia* and the genera *Platycarpum* and *Henriquezia* may give us with regard to the taxonomical position of these genera, it will be well to pay some attention to the points of resemblance in order to find out whether the latter do not invalidate the conclusions we have arrived at.

The main points of resemblance between the three genera are found in the large size of the pollen grains, a feature to which, as we have already pointed out, not much value can be attached, in the absence of endosperm in the ripe seed, in the structure of the embryo with its large cotyledons and its small axial part, in the shape and mode of dehiscence of the capsule, in the structure of the testa, in the pattern formed by the stomata and the surrounding epidermis cells on the lower side of the leaf, and in the presence of large resin cells in the twigs just outside the cambium.

Exalbuminous seeds were so far not known in any of the subfamilies of the *Rubiaceae*, although the amount of endosperm in the seeds of the *Guettardoideae* is but small, the embryo being of a larger size than is usual in the family. That the seeds of *Gleasonia*, *Platycarpum* and *Henriquezia* agree with each other in being exalbuminous, means that we experience with each of these genera in this respect the same difficulty when we try to find a place for them among the *Rubiaceae*, but as exalbuminous seeds occur in widely different circles of affinity, it certainly does not mean that they should of necessity be regarded as nearly allied.

That the cotyledons are very large in comparison with the axial part of the embryo is another feature on account of which it is difficult to find for these genera a place among the *Rubiaceae*, for even where in the embryo of plants belonging to this family fairly large cotyledons are noted, as in the genus *Simira* Aubl. (*Sickingia* Willd.), they prove to be hardly longer than the axial part. Howsoever this may be, this feature too can not be taken as proof of a near affinity between *Gleasonia* and the genera *Platycarpum* and *Henriquezia*, as embryos of this kind are certainly not confined to a single taxonomical group.

The resemblance in the shape of the capsule and in its mode of dehiscence need not detain us very long. The resemblance in shape is rather superficial, for the capsule of *Gleasonia* is completely inferior and by no means so strongly flattened as the semi-superior or entirely superior capsules of the two other genera, and the resemblance in the mode of dehiscence, which in all three is loculicidal, is taxonomically of no importance, as loculicidal capsules return in almost every order of the Angiosperms.

The resemblance in the structure of the testa, by which I was originally so strongly impressed that I overemphasized its taxonomical importance, appears now, after a more detailed investigation, to be of a rather superficial nature. It is true that in all three the genera the walls of the testa cells are strengthened by a network of thickenings, but this network is in *Gleasonia* met with in the convex outer wall and the lateral ones, whereas it is found in the two other genera on the basal wall; however, it must be admitted that, at least in *Platycarpum*, it is also present in the papillae, which are part of the outer wall. However, as testa cells with reticulate walls return in very different families, their taxonomical importance should not be overrated. It can not even be adduced as an argument for excluding these genera from the *Rubiaceae*, as in the genus *Hillia* Jacq. too the testa consists of reticulate cells.

The position of the stomata with regard to the surrounding epidermis cells on the underside of the leaf is in all three genera the same (Fig. 8). The pattern they form with these cells is the one that is typical for the *Rubiaceae*. This, however, does not prove that they belong to this family, for this pattern is not confined to it. It returns e.g. in some of the *Bignoniaceae*, i.e. in a family to which two of the three genera are supposed to be allied.

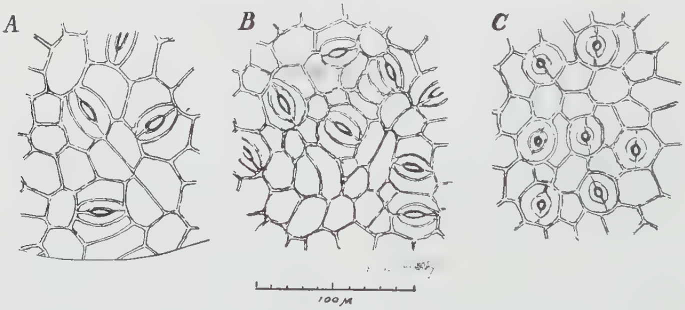

Fig. 8. Epidermis on the underside of the leaf of A. *Gleasonia macrocalyx*, B. *Platycarpum negrense*, and C. *Henriquezia verticillata*.

The presence of very large resin cells in the phloem is a similar character. Although such cells are apparently not of common occurrence in the *Rubiaceae*, they are not unknown in that family; they are found e.g. in the *Gardenieae*. They occur also in several other families. Precise knowledge with regard to these structures is, however, difficult to obtain, as herbarium specimens are not very suitable for their study.

Besides the points in which *Gleasonia* resembles *Platycarpum* as well as *Henriquezia* there is also a point in which it resembles only one of them, viz. *Platycarpum*. It is a very striking one, and it is found in the stipules which in both these genera are large and intrapetiolar. Especially the intrapetiolar position is a most remarkable feature, for intrapetiolar stipules, although at one time thought to be not uncommon in the *Rubiaceae*, are in reality, as I have pointed out at an earlier occasion (Bull. Jard. Bot. Buitenz. Sèr. 3: *13*: 425. 1935) very rare. In fact, among the genera in which they had been recorded in the older literature *Capirona* Spruce ex Bth. proved to be the only one in which they are actually present. I must admit, however, that the description of *Gleasonia* was at that time overlooked by me, and add that with regard to the stipules of *Platycarpum* no reliable information was as yet available. I myself found them at that time in *Didymoecium* Brem. and recently also in *Suteria* DC. It is noteworthy that these genera belong to different tribes and partly even to different subfamilies, and that neither *Gleasonia* nor *Platycarpum* show in other respects a well-marked resemblance to any one of them. The taxonomical value of the intrapetiolar stipules must therefore be regarded as very small, and their presence in *Gleasonia* as well as in *Platycarpum* can therefore hardly be interpreted as indicating affinity between them. It seems that we are confronted here with a mere analogy, and this supposition finds support in the fact that the intrapetiolar stipules of *Platycarpum* appear to owe their origin to the splitting of an originally closed sheath, whereas those of *Gleasonia* seem to be free from the start. The stipules of *Gleasonia*, moreover, differ, as we have already seen, fundamentally from those of *Platycarpum* in the presence of colleters. In the absence of the latter there is complete agreement between the stipules of *Platycarpum* and those of *Henriquezia*, which at first sight look quite different, in the first place because they are rather narrow, and in the second place because there are two of them to each leaf. There is, however, agreement in so far that in *Henriquezia* too the stipules are at first united into a sheath which completely envelops the terminal bud.

THE POSITION OF THE GENUS *Gleasonia*

If we try to determine the position of the genus *Gleasonia* by the aid of the data given above, we come to the conclusion that the latter agrees in most of its characters with the notion we have, in the course of time, arrived at with regard to the family *Rubiaceae*; especially important in this respect are the decussate leaves, the stipules provided with colleters, the actinomorphous flowers with inferior ovary and sympetalous corolla, and the simple whorl of stamens alternating with the corolla lobes. The points in which it deviates from our notion of this family are the exalbuminous seeds, the structure of the embryo with its large cotyledons and comparatively small axis, and also, though this seems to be of somewhat less importance, in the large size of the pollen grains. The problem with which we are confronted, may therefore be formulated in this way: should we extend the limits of the family *Rubiaceae* so far that it becomes possible to include the aberrant genus *Gleasonia*, or is it preferable to create for this genus a new family?

The absence of endosperm is doubtless a character of great taxonomical importance. It is true that the amount may vary to some extent in a definite group, as it does e.g. in the *Rubiaceae* themselves, where we have one subfamily, the *Guettardoideae*, with but a comparatively thin layer of it, but the difference between albuminous and exalbuminous seeds is nevertheless, as a rule, well-marked, and it happens but rarely that one has any difficulty in deciding to what category a seed should be referred. Moreover, up to a certain rank we find in taxonomically well-defined groups, as a rule, but one of these kinds of seed. That the seeds of *Gleasonia* are undoubtedly exalbuminous, is therefore a strong argument for removing this genus from the *Rubiaceae*. If we will not go that length, we will have to widen the delimitation of the family, for as there is no place for our genus in any of the subfamilies, a new one will have to be created, and to make place for the latter, the limits of the family will have to be extended. If we decide that the delimitation of the family is better left unchanged, we will, of course, first of all have to find out whether there is a place for the genus in one of the other families of the *Rubiales*, for in view of the important points of resemblance with the *Rubiaceae* s.s. it need not be doubted that it belongs to this order. As there is here but one family with exalbuminous seeds, viz. the *Valerianaceae*, this question is easily settled: in the *Valerianaceae* there is certainly no place for our genus as the latter have exstipulate leaves and zygomorphous flowers with an incomplete androecium and gynoecium. The great taxonomical value of the points of resemblance between *Gleasonia* and the *Rubiaceae* creates a strong link between them, and brings them in opposition to the rest of the *Rubiales*, which means that they form a group that would have to be recognized as a suborder. For this reason we might formulate our problem also in this way: should we create for *Gleasonia* a new family, and for the latter and the *Rubiaceae* s.s. a new suborder, or should we leave the genus in the *Rubiaceae*, of which in this case the delimitation should be widened?

In order to find a solution for the problem formulated in the preceding paragraph, we will have to find out whether the differences between *Gleasonia* and the subfamilies that so far have been recognized within the *Rubiaceae*, are of greater taxonomical importance than those existing between any two of them, for if the differences between some of the latter would prove to be of greater importance, there would certainly be no reason to create a new family for *Gleasonia*. If, on the other hand, the differences between these subfamilies would prove to be of less importance than those between *Gleasonia* and the whole group, then the creation of a mere subfamily would hardly be sufficient.

The main points in which *Gleasonia* differs from the whole set of subfamilies are the exalbuminous seed and the structure of the embryo with its large cotyledons and short axis. It differs moreover from the

Cinchonoideae sensu meo in the absence of the large oval or orbicular pits on the basal walls of the testa cells, from the *Urophylloideae* by the much thinner, not finely perforated walls of the testa cells, from the *Ophiorrhizoideae* in the absence of the peculiar wartlets on the walls of the testa cells, from the *Guettardoideae* in the entirely different fruit and also in the absence of crystals of calcium oxalate in the walls of the hairs by which the various parts are covered, from the *Ixoroideae* in the totally different structure of the upper part of the style, which does not function as "receptaculum pollinis", and from the *Rubioideae* by the absence of raphides.

That *Gleasonia* is fundamentally different from each of the subfamilies that hitherto have been recognized in the *Rubiaceae*, can therefore not be doubted, and when we were to obey our first impulse, we would hardly hesitate to decide that it is more fundamentally different from the whole set than any two of them are from each other. We should realize, however, that all these subfamilies consist of more than one genus, most of them even of a very large number, and that the differences between them would doubtless be more numerous and therefore more impressive if each of them was represented, like the group to which *Gleasonia* belongs, by a single genus only. For this reason it seems hardly possible to decide the question in an entirely objective way, and as the introduction of a new subfamily answers our present needs, and will probably meet with less resistance than the introduction of a new family would do, it seems prudent for the time being to go no further.

The exposition given above is summarized in the following description of the new subfamily.

Gleasonioideae nova subfamilia *Rubiacearum* a subfamiliis aliis seminibus exalbuminosis et embryone cotyledonibus parte axili majoribus instructo faciliter distinguenda.

Arbores. Folia opposita, petiolata. Stipulae magnae, intrapetiolares, simplices. Inflorescentiae terminales, corymbi- vel paniculiformes. Flores pentameri, actinomorphi, magni. Ovarium biloculare, utroque loculo ovulis pluribus instructo; ovula in serie verticali duplici dimidio inferiore septi inserta. Calyx regularis, in lobos longos partitus; lobi albi, post anthesin decidui. Corolla satis magna, extus sericea, tubo infundibuliformi sensim in faucem ampliato, lobis aestivatione induplicativa. Stamina fauce inserta; antherae exsertae. Granula pollinis tricolpata, magna, in tetrades unita. Stylus in stigmata dua exeuns, breviter exsertus. Fructus (Fig. 9) capsula complanata, loculicide dehiscens, utroque loculo seminibus pluribus instructa. Semina angulosa, exalbuminosa; embryo cotyledonibus crassis parte axili majoribus instructus; testa e cellulis convexis composita, pariete externa reticulatione laxa invigorata.

Subfamilia adhuc e genere unico constans, Americae Tropicalis incola.

As this subfamily comprises but a single genus, it also contains but a single tribe. It seems superfluous to describe the latter; if it should receive a name, this, of course, would have to be **Gleasonieae.**

The genus *Gleasonia* Standl. comprises at present three species, *Gl.*

duidana Standl., *Gl. uaupensis* Ducke and *Gl. macrocalyx* Ducke, all three confined to Tropical South America, the first to Amazonian Venezuela, the two others to Amazonian Brazil. *Gl. duidana* and *Gl. uaupensis* are now comparatively well-known; they are doubtless nearly related species, differing but slightly in the length of the petioles, the size of the leafblade and of the stipules, the length and width of the calyx lobes, the size of the corolla, the size of the pollen grains (cf. p. 356) and the structure of the testa; *Gl. uaupensis*, moreover, is, as Ducke already reported, a myrmecophilous species, the concave stipules sheltering small red ants. The third species, *Gl. macrocalyx*, differs conspicuously from the two others in the absence of the hirsute indumentum, in the much larger size of the fruit, and in the presence of wartlets on the testa; this species is unfortunately still very imperfectly known. As in all specimens that so far have been collected, the corolla had already been shed, and as none of them were provided with fully ripe fruits, the very important characters of the pollen and of the mature testa could not yet be studied. So long as these characters are unknown, it is hardly possible to decide whether this species really belongs to the genus *Gleasonia*. However, as its seeds are exalbuminous and as its embryo is provided with large cotyledons, it is not to be expected that it will have to be referred to another subfamily.

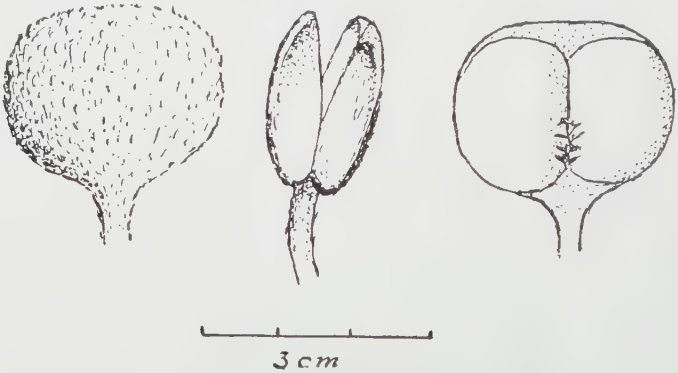

Fig. 9. Capsule of *Gleasonia uaupensis*.

THE POSITION OF THE GENERA *Platycarpum* AND *Henriquezia*

The absence of endosperm and the large size the cotyledons reach in comparison with the axial part of the embryo are two important characters in which, as we have seen, the genera *Platycarpum* and *Henriquezia* resemble *Gleasonia* and in which they all three differ from the general plan of the *Rubiaceae*, but *Platycarpum* and *Henriquezia* differ from the latter also in some important points in which *Gleasonia* is consistent with it. These points are 1) the absence of colleters on the inside of the stipules, 2) the presence of a band of hairs on the ventral side of the corolla throat and the distinctly zygomorphous androecium, and 3) the semi-superior or even almost completely superior capsule. Each of these deviations from the general plan would already in itself form an important argument against the inclusion of these genera, but put together their weight becomes so overwhelming that it will crush every attempt in this direction. The presence of a strip of hairs on the ventral side of the corolla throat and the distinctly zygomorphous androecium, moreover, point towards an entirely different circle of affinity, viz. that of the *Tubiflorae*, where we find in the *Bignoniaceae*, *Pedaliaceae*, *Thunbergiaceae*, *Mendonciaceae* and *Acanthaceae* a group of families with which the genera *Platycarpum* and *Henriquezia* show a quite remarkable resemblance in habit; in fact, this resemblance is much more pronounced than that with the *Rubiaceae*.

When HUMBOLD and BONPLAND described the genus *Platycarpum* (Plantae aequinoctiales 2: 81, tab. 104. 1809) they were apparently so impressed by the resemblance meant in the preceding paragraph that they placed their new genus without any hesitation in the *Bignoniaceae*. On account of the inferior ovary, the position of the ovules and the presence of stipules, this is, of course, an unacceptable decision, but these characters were either misunderstood or overlooked by them. It can not be doubted that they regarded the ovary as superior, for they described the calyx as inferior, probably because they found the scar of the latter near the base of the capsule, and did not realize that by far the greater part of the latter owes its origin to the very strong development of the portion inside the calyx; and that they overlooked the presence of stipules is also easily comprehensible, as the latter are early deciduous and, as a rule, present only round the terminal bud; it is quite possible that all the branches they had collected ended in inflorescences, and in that case probably not a single stipule would have been present. That the seeds are described as provided with a membranaceous margin, is not correct either; it applies only to young seeds where the space inside the testa is not yet completely filled up by the embryo. A similar mistake was made by Bentham when he described the seeds of *Henriquezia* as marginate, though to be quite fair to him I must admit that he cautiously added the words "ut videtur". Here too in the fully mature seeds the whole space inside the testa is occupied by the embryo, and there is no trace of a wing. J. D. HOOKER (in BENTHAM et HOOKER, Gen. Pl. 2: 12. 1873), to be sure, was entirely mistaken when he described the seeds of the *Henriquezieae*, the tribe created by him for the reception of the genera *Henriquezia* and *Platycarpum*, as "latissime alata".

The authors who like FENZL (Denkschr. d. k. bayer. bot. Gesellsch. 3: 239 et 265. 1841), DE CANDOLLE (Prodr. 9: 233. 1845) and BUREAU (Monographie des Bignoniacées: 80–81 et 103. Paris 1864) in the next half century occupied themselves with *Platycarpum*, accepted Humbold and Bonpland's classification, but they too overlooked the presence of stipules and the inferior position of the ovary.

When BENTHAM described his new genus *Henriquezia* (Kew Journ. of Bot. 6: 337. 1854), he duly mentioned its near affinity with *Platycarpum*, and referred it, just as his predecessors had done with the latter, to the *Bignoniaceae*, and like them he failed to specify his reasons. It is well to remember this when we look at the arguments he adduced in support of his view that the two genera are nearly allied. They read as follows: "The five equal and perfect stamens, and the short broad fruit with very few seeds, are the same, as well as the general habit and simple leaves." If the two genera really belonged to the *Bignoniaceae*, these characters would suffice to contrast them with the rest of the family, and this in its turn would bring them in closer contact with each other. However, as soon as we drop the notion that they belong to this family, these characters loose a great deal of their value, for then they appear to be features of a rather general nature, which return in very different circles of affinity. This applies especially to the first-named characters, the five perfect stamens and the simple leaves, but even the presence of short and broad fruits with a small number of seeds can not be regarded as a very special character, and it looses, moreover, much of its value when we realize that the capsules of the two genera are in other respects quite different, for that of *Platycarpum* proves to be almost completely superior and in dehiscence the right and left half of each valve fold backwards until they meet, whereas the capsule of *Henriquezia* is only semi-superior and its valves in separating do not appreciably change their form. This difference in the mode of dehiscence was unknown to the earlier authors who had no ripe fruits at their disposition. When Bentham said that the stamens in the two genera are all equal, he was mistaken, for they are in reality quite distinctly unequal. It is rather unfortunate that this inequality escaped his attention, and also that the overlooked the bent at the base of the filaments, for the presence of a zygomorphous androecium of this kind is one of the most important points of resemblance between these genera and the *Bignoniaceae* and their nearest allies.

The more important points of resemblance between *Henriquezia* and *Platycarpum* were omitted by Bentham, partly, no doubt, because he regarded them as general characters of the *Bignoniaceae*, the family to which the genera were referred by him, and partly, because they were overlooked. To the first group apparently belong the flat, exalbuminous seeds, which erroneously were regarded as winged, and the structure of the embryo with its large and flat cotyledons; to the second the remarkable "glands" at the base of the petiole, the presence of stipules, the complete but distinctly zygomorphous androecium, and the collateral ovules. That he overlooked the importance of the petiolar "gland" is rather surprising, because the presence of this organ is in his description of *Henriquezia verticillata* duly recorded; that he would have overlooked its presence in *Platycarpum*, seems therefore hardly possible. I suppose that the omission was merely accidental.

The way in which he summarizes the points of difference between the two genera is not very satisfactory either. According to him *Henriquezia* differs from *Platycarpum* in "the semi-adherent calyx with a persistent base and only four lobes, and the shape of the corolla, so much more Bignoniaceous than that of *Platycarpum*". The calyx, however, is not semi-adherent but totally adherent; only when the fruit begins to grow out, the calyx gradually shifts from the top to a position midway between the latter and the base; and its base can hardly be called persistent: in this respect I see no difference at all between the two genera. That some of the *Platycarpum* species too possess but four calyx lobes, he could not know, as these species had not yet been collected. The corolla of *Henriquezia* is much larger than that of *Platycarpum*, but in shape it is hardly different from the latter. The really important points of difference were as yet overlooked; they are found in the nature of the stipules, in the number of ovules and in the characters of the fruit. The stipules of *Henriquezia* are narrow and there are two of them to each petiole, those of *Platycarpum* are wide and intrapetiolar; in *Henriquezia* they are, moreover, inserted on the petioles and shed with the latter, whereas in *Platycarpum* they are inserted on the stem, and leave a scar that surrounds the stem and passes above the base of the petioles. The ovary cells of *Henriquezia* contain four ovules, those of *Platycarpum* two. The capsule of *Henriquezia* is semi-superior, oblate-lenticular, and provided with valves that after dehiscence retain their shape, whereas that of *Platycarpum* is almost completely superior, discoid, and provided with valves of which the right and left half after dehiscence fold back until they meet.

J. D. HOOKER (in BENTHAM et HOOKER, Gen. Pl. 2: 12. 1873) accepted Bentham's view with regard to the near affinity between the two genera, and brought this out by uniting them into a tribe, for which he introduced the name *Henriquezieae*. He differed, however, from Bentham and the latter's predecessors with regard to the place that would have to be assigned to them, and instead of to the *Bignoniaceae* he referred his new tribe to the *Rubiaceae*. It is not quite clear why he did this, for the points in which they differ from the general plan of this family and in which they agree with the *Bignoniaceae*, the zygomorphous corolla and the exalbuminous seeds, are duly mentioned in his description. The zygomorphism of the flower is even somewhat overemphasized, for the corolla is described as bilabiate, whereas the lobes are in reality but slightly unequal and certainly not united into an upper and a lower lip. The very distinct zygomorphism of the androecium, on the other hand, is not specially mentioned. We must assume therefore that he did not attach much weight to these characters, and thought the position of the ovary, which he described as semi-superior, and the presence of stipules, which he was the first to mention, of greater importance. That this would be so, however, seems very dubious, for semi-superior and even entirely inferior ovaries, although not present in the *Bignoniaceae* themselves, are not unknown in the order to which the latter belong. As Bentham already remarked, they occur in one of the subfamilies of the *Gesneriaceae*. Stipules, it is true, do not occur in this order, but as their distribution in the various orders is rather erratic, their presence can not be regarded as a sufficient ground to exclude these genera from an order in which stipules were so far regarded as absent.

The diagnostic characters which Hooker mentioned in his key to the genera, have been taken from the calyx. *Henriquezia* is characterized by "Calycis limbus circumscisse deciduus" and *Platycarpum* by "Calycis limbus 5-lobus". The expression "circumscisse deciduus" is not quite clear. I can not believe that it refers to the way in which the upper part of the calyx is separated from the hardly noticeable base, for in this respect there is not much difference with *Platycarpum*; I prefer to suppose that it refers to the scar left by the calyx on the surface of the fruit; this scar is found midway between the top and the base, i.e. in the place where a "capsula circumscissa" would open: in the position of this scar there is indeed a very marked difference between the two genera, for in *Platycarpum* it is found quite near to the top of the pedicel. That in *Platycarpum* too species with four calyx lobes are found, was, as mentioned above, in Hooker's time unknown.

SCHUMANN (in Fl. Bras. VI, 6: 133. 1889 and in ENGLER and PRANTL, Nat. Pflanzenfam. IV, 14: 39. 1891) adopted Hooker's classification, but he too failed to make this decision clear. Nevertheless he seems to have felt the difficulty caused by the zygomorphism of the flower, for in this light I wish to see his remark that Hooker's *Henriquezieae* form by means of some other genera with zygomorphous flowers, like *Capirona*, *Coutarea* and *Ferdinandusa*, a link between the *Cinchoneae* and the *Bignoniaceae*. This is, if taken literally, a rather strange assertion, for it presupposes that the kind of zygomorphism found in the flowers of the *Bignoniaceae* and in those of *Platycarpum* and *Henriquezia* is homologous with the zygomorphism shown by the flowers of *Capirona*, *Coutarea* and *Ferdinandusa*. However, that a character found in one order in part of the genera of a single family can be regarded as homologous with a character observed in a family belonging to a different order, is certainly a rare exception, for it demands that the character is part of the general plan of the next higher unit, viz. the one that comprises both these orders; in our case this is hardly to be expected. Moreover, the resemblance between the zygomorphism shown by the flowers of the *Bignoniaceae* and of *Platycarpum* and *Henriquezia* and that seen in the flowers of *Capirona*, *Coutarea* and *Ferdinandusa* is very superficial indeed, and can therefore not be regarded as indicating homology. The most characteristic features of the zygomorphism shown by the flowers of the *Bignoniaceae* and of *Platycarpum* and *Henriquezia* are found in the insertion of the stamens at different height and in the bent at the base of the filaments, and these features are completely absent in the flowers of *Capirona*, *Coutarea* and *Ferdinandusa*, where the zygomorphism is confined to a slight curvature of the corolla and a corresponding difference in the length of the filaments. The first kind of zygomorphism is characteristic for a large part of the *Tubiflorae*, whereas the second is but a slight modification of the actinomorphism that is typical for the *Rubiales*. The zygomorphism of *Platycarpum* and *Henriquezia* is therefore no link between that of the *Bignoniaceae* and that of the genera *Capirona*, *Coutarea* and

Ferdinandusa and via the latter with the actinomorphism of the other *Rubiaceae*, but it is fully identical with that of the *Bignoniaceae* and quite different from that of *Capirona*, *Coutarea* and *Ferdinandusa*.

The characters used by Schumann in his key to the genera, viz. for *Platycarpum* "Flowers nearly hypocrateriform, vertical. Calyx lobes singly deciduous. Leaves decussate", and for *Henriquezia* "Flowers bilabiate, horizontal. Calyx circumscissile. Leaves verticillate", are inadequate. Neither in the shape of the corolla nor in the position of the flower any well-marked difference is observable; the calyx is shed in both genera in the same way; and species with verticillate leaves are, as we now know, found in *Platycarpum* too.

In his monograph of the genus *Platycarpum* STEYERMARK (Am. Journ. of Bot. 39: 418–429. 1952) also followed Hooker in referring the *Henriquezieae* to the *Rubiaceae*, but he too gave no arguments. In his key to the genera he introduced a new diagnostic character, viz. the number of ovules in the ovary cells, 2 in *Platycarpum*, 4 in *Henriquezia*. This is a reliable difference, though less easily discernible than the differences in the stipules (*Pl.*: as many as the leaves and wide; *H.*: twice as many as the leaves and narrow) and in the capsule (*Pl.*: discoid and almost entirely superior, the right and left half of each valve folding back until they meet; and *H.*: oblate-lenticular and semi-superior, the right and left half of the valves not folding back), which are not mentioned.

From this survey of the literature and from the remarks I have inserted here and there we may conclude that the genera *Platycarpum* and *Henriquezia* are near enough to each other and at the same time sufficiently distinct from other genera to be united into a taxonomical group to which at least the rank of a tribe will have to be assigned. Further it seems clear that this group can not be inserted in the *Bignoniaceae*, as they differ from the latter in such important points as the inferior ovary, the collateral ovules and the presence of stipules. The peculiar kind of zygomorphism shown by the flower, however, suggests a nearer affinity with this family than with the family *Rubiaceae*, to which they were referred by Hooker. From the general plan of the latter they differ not only in the presence of the strip of hairs on the ventral side of the corolla throat and in the zygomorphism of the androecium but also in the absence of colleters on the inside of the stipules, in the exalbuminous seeds and in the structure of the embryo with its large cotyledons and small axial part. The two latter characters are found also in the genus *Gleasonia*, which, as we have pointed out, is to be referred either to the *Rubiaceae* themselves or else to a very closely related family, and their presence in the *Henriquezieae* can therefore not be regarded as a factor of decisive importance, but the combination of the first-named characters, the peculiar kind of zygomorphism which finds its expression in the presence of a strip of hairs on the ventral side of the corolla throat and in the zygomorphous androecium, and the absence of colleters, is doubtless of so outstanding significance that it fully justifies the exclusion of these genera from the *Rubiaceae*. The peculiar type of zygomorphism exhibited by their flowers, moreover, points in a different direction, viz. in that of the *Tubiflorae.*

The presence of an inferior ovary makes it impossible to return the group to the *Bignoniaceae*, but it does not prevent us from referring it to the order of which the latter form a part, as in one of the other families, the *Gesneriaceae*, such ovaries are by no means uncommon. The collateral ovules form no obstacle either, as this kind of arrangement of the ovules is certainly not unknown in the *Tubiflorae;* it occurs here in two families that are to be regarded as near allies of the *Bignoniaceae*, viz. the *Thunbergiaceae* and the *Mendonciaceae*, and also in the *Labiatae*. The presence of stipules might seem, at first sight, to offer a greater difficulty, as stipules are indeed entirely unknown in the *Tubiflorae*, but we should realize that the groups in which they occur, are of very different taxonomical rank, and that they are rather irregularly spread over the various orders. That the *Tubiflorae* were so far regarded as an order in which stipules are absent, is therefore no sufficient ground for excluding a group in which they are present.

That the genera *Platycarpum* and *Henriquezia* can not belong to the *Rubiaceae*, would not necessarily mean that there is no place for them in the *Rubiales*, i.e. in the order to which the *Rubiaceae* belong. This is doubtless a possibility that deserves careful consideration. It is certainly easy to see that they can not belong to one of the families that so far have been recognized in this order, for there is only one among them that agrees with our genera in the presence of exalbuminous seeds, and this family, the *Valerianaceae*, differs from them in the exstipulate leaves and in the incomplete androecium and gynoecium. The possibility that they might form a distinct family is, on the other hand, not so easily discarded, as the order is but poorly defined, so that it is difficult to say what might or might not belong to it. At any rate, as the *Rubiaceae* are the only family with some of whose representatives our two genera show a certain resemblance, and as this resemblance may, on good grounds, be regarded as a mere analogy, the insertion of such a new family in this order can not be regarded as a plausible solution of our problem. The peculiar type of zygomorphism shown by the flowers of our two genera is, at any rate, a feature that looks entirely out of place in this order.

The foregoing considerations lead to the conclusion that the genera *Platycarpum* and *Henriquezia* form a well-defined group, for which there seems to be no place in the *Rubiales*, but which fits very well into the order *Tubiflorae*, although it can apparently not be referred to one of the families that so far have been recognized. On account of the large exalbuminous seeds it would have to be referred to a position in the neighbourhood of the *Bignoniaceae*, *Pedaliaceae*, *Martyniaceae*, *Thunbergiaceae*, *Mendonciaceae* and *Acanthaceae;* in the structure of the pollen grains there is moreover some resemblance with the *Pedaliaceae* and the *Bignoniaceae;* in the collateral ovules with the *Thunbergiaceae* and the *Mendonciaceae;* in habit and especially in the form of the fruit, which is flattened perpendicular to the dissepiment, they remind one, as Fenzl already remarked, of the *Tecomeae* (*Bigno-*

niaceae); and in the large and flat, wingless seeds of some of the *Pedaliaceae*.

The genera *Platycarpum* and *Henriquezia* therefore are to be united into a group that will have to receive the rank of a family, and for which a place will have to be found in the order *Tubiflorae*. As the two genera were already united by Hooker into a tribe *Henriquezieae*, the name *Henriqueziaceae* seems to be indicated for this family. It is true that Hooker might perhaps better have derived the name for his tribe from *Platycarpum*, as that name has much older rights than *Henriquezia*. In fact, some years later BAILLON too (Hist. d. Pl. 7: 345 et 487. 1880) united the genera into a group, but as he judged the differences between them of minor importance, he did not regard this group as a tribe but as a genus, and for this genus he had, of course, to use the name *Platycarpum*. This means that if Baillon's view were to be accepted, the name of the tribe as well as that of the family would have to be derived from *Platycarpum*. However, as there is no reason to assume that later botanists will return to Baillon's standpoint, it seems safe to base the name of the family on that of Hooker's tribe. The family may be described as follows:

Henriqueziaceae familia nova *Tubiflorarum* praesentia stipularum et "glandulae petiolaris" a familiis aliis diversa, seminibus exalbuminosis ad *Bignoniaceas*, *Pedaliaceas*, *Martyniaceas*, *Thunbergiaceas*, *Mendonciaceas* et *Acanthaceas* accedens sed ab eis absque stipulis et glandula petiolari ovario infero distincta, structura pollinis cum *Bignoniaceis* et *Pedaliaceis*, ovulis collateralibus cum *Thunbergiaceis* et *Mendonciaceis* congruens, habitu et forma capsularum inter *Bignoniaceas Tecomeis* nonnullis, seminibus complanatis et exalatis *Pedaliaceis* aliquibus comparanda.

Arbores parvae vel mediocres. Folia decussata vel verticillata, petiolata et stipulata, simplicia et integerrima; petiolus ad basin dorso "glandula" laevi, sicc. nigrescente instructus. Stipulae sine colletris. Flores in inflorescentias terminales, paniculiformes dispositi. Ovarium inferum, biloculare, utroque loculo ovulis 2–4 collateralibus instructum. Calyx fere ad basin 4- vel 5-partitus, post anthesin deciduus. Corolla semper 5-mera, paulum zygomorpha, extus pubescens, tubo in faucem campanulatam ampliato, intus ad insertionem staminum barbato et virga pilorum e basi lobi mediani descendente percurso, lobis subaequalibus obtusis, aestivatione adscendente imbricatis. Stamina 5 ad altitudines inaequales inserta, inclusa; filamenta basi curvata, inaequilonga; antherae dorsifixae, basi sagittatae, loculis parallelis. Granula pollinis satis magna, colpis 3 6 instructa. Discus annularis. Stylus glaber, ad altitudinem antherarum in stigmata 2 exeuns. Capsula semi-supera et oblato-lenticularis vel fere tota supera et discoidea, dissepimento angusto instructa, loculicide dehiscens, utroque loculo semina 2 vel 4 continens. Semina valde complanata sed exalata, exalbuminosa, cellulis testae in papillas exeuntibus; embryo cotyledonibus planis et magnis et axi brevi instructus.

Generibus 2 in parte Americae Tropicalis Amazonica dicta distributa.

The two genera are easily distinguishable by means of the differences given in the following key.

Key to the Genera of the *Henriqueziaceae*

1. Stipules as many as leaves, inserted on the stem, intrapetiolar and ovate. Flowers comparatively small, i.e. corolla less than 2 cm long. Ovary cells with 2 ovules. Pollen grains 3- or 4-colpate (Fig. 4). Capsule discoid, almost entirely superior, i.e. the scars of calyx and corolla near the top of the pedicel; valves consisting of a right and left half which after dehiscence fold back until they meet (Fig. 10). Testa cells with straight walls (Fig. 5) . . . . *Platycarpum*

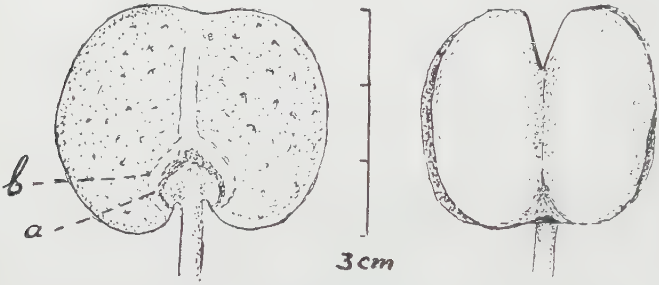

Fig. 10. Capsule of *Platycarpum orinocense* before and after dehiscence; a. scar of calyx; b. scar of corolla.

1: Stipules twice as many as leaves, inserted on the petioles, linear. Flowers large, i.e. corolla more than 3 cm long. Ovary cells with 3 or 4 ovules. Pollen grains 5- or 6- colpate (Fig. 4). Capsule oblate-lenticular, semi-superior, i.e. the scar of the calyx midway between the top and the base, and that of the corolla midway between the top and the scar left by the calyx; valves not consisting of mobile halves (Fig. 11). Testa cells with undulating walls (Fig. 6) . . . . *Henriquezia*

There are still a number of species of which flower and fruit are either unknown or but imperfectly known. However, in view of the great uniformity shown by those that could be studied in sufficient detail, there seems to be good reason to expect that the other ones will not deviate too much. Still, with regard to the characters of the pollen grains and especially of the testa cells some reserve should be made, as the pollen grains could be studied only in a small number of species, and as in the genus *Henriquezia* seeds were available only from the type species. The most reliable characters nevertheless are those of the stipules, and the latter are also the most useful ones, as they may serve even when neither flowers nor fruits are available; even when they themselves have been shed, their scar can enlighten us with regard to the position they occupied, and this is enough.

In the structure of the pollen grains the difference seems to be greater than the key indicates, for, as the figures show, they differ not only in the number of colpae but also in size, outline and relief.

It does not seem necessary to give new latin descriptions of the two genera, for although the existing ones are not entirely satisfactory, they can easily be extended and corrected by means of the data contained in the key and in the description of the family.

The genus *Platycarpum* was not so long ago revised by STEYERMARK l.c., who brought the number of species to five. A sixth species will be described below, and of a seventh species material was collected

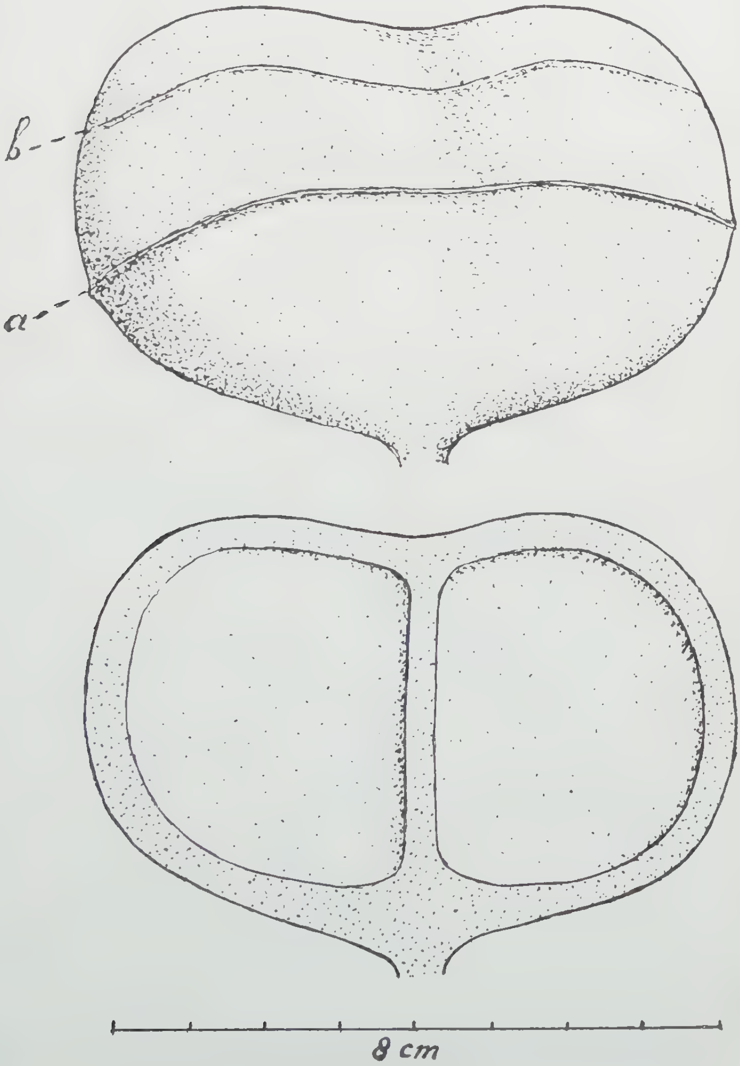

Fig. 11. Capsule of *Henriquezia verticillata*; a. scar of calyx; b. scar of corolla.

in British Guiana (Paharaina Mts, Mt Ayanganna, Maguire e.a. 40666 NY); it resembles *Pl. Duckei* Steyermark, but has much larger capsules; as no flowers were available, it seems better to leave it unnamed.

Steyermark based his key to the species mainly on the presence or absence of an indumentum, and on the latter's distribution and quality. It is not to be expected that this will lead to a fully natural classification, but in view of the near affinity between the species, a better arrangement will probably be difficult to obtain, and it can not be denied that the species that so far have been described, are in this way easily identifiable. Moreover, it was the only way that was open to him, as he had to include his *Pl. decipiens*, of which neither flowers nor fruits are known. My own *Pl. Froesii* could easily find a place in his key; to this end we would have to insert before his division leading to *Pl. orinocense* and *Pl. Duckei* another one contrasting these two species on account of their opposite leaves with *Pl. Froesii*, whose leaves are ternate.

One might perhaps have preferred to base the key in the first instance on the number of calyx lobes, were it not for *Pl. decipiens*, which in this case could not have been placed, as its calyx is unknown. The species with 5-merous calyx are *Pl. orinocense*, *Pl. negrense* and *Pl. Froessii*, those with 4-merous calyx *Pl. Duckei* and *Pl. rhododactylum;* in both these groups there is one species with ternate leaves, in the first *Pl. Froesii*, and in the second *Pl. rhododactylum*. It is possible, however, that the taxonomical value of the difference in the number of calyx lobes is not so high as one might be inclined to suppose; in *Pl. orinocense* the number of calyx lobes seems to vary, and such variability is, of course, not easily reconcilable with our idea of a taxonomically important character. It is perhaps worth noting that a comparison of the position the calyx lobes occupy in the 4-merous and in the 5-merous calyx, leads to the conclusion that the anterior lobe of the 4-merous calyx is homologous with the two anterior ones of the 5-merous calyx.

The new species may be described as follows:

Platycarpum Froesii Brem. n. spec. foliis ternatis cum *Pl. rhododactylo* Woodson et Steyermark congruens, sed calyce 5-mero et foliis minoribus, supra scabridis et subtus molliter pubescentibus, numero minore nervorum percursis ab eo faciliter distinguenda, calyce 5-mero et foliis parvis ad *Pl. negrense* Ducke accedens, sed foliis ternatis supra scabridis et subtus pubescentibus, inflorescentia tomentella ab eo diversa, a *Pl. orinocensi* Humb. et Bonpl., ad quem calyce 5-mero et indumento foliorum accedit, foliis et ternatis et minoribus, numero minore nervorum percursis recedens.

Arbor parva, circ. 4 m alta. Ramuli novelli ferrugineo-tomentosi, veteriores cortice nigrescente, sicc. plicatulo vestiti. Folia ternata; petiolus glandula basali excepta ferrugineo-tomentosus, 2–4 mm longus; lamina oblonga, 6.5–8.5 cm longa et 2.2–3.8 cm lata, apice obtusa, basi acuta, margine recurvata, coriacea, paulum discolor, sicc. brunnescens, supra costa dense strigosa excepta primum pilis satis longis sparsa, mox pilis rejectis scabrida, subtus costa tomentella, nervis venulisque pubescens, costa subtus prominente, nervis utroque latere costae 11 vel 12 subtus prominulis, venulis dense reticulatis utrimque distinguendis. Stipularum calyptra longe ferrugineo-villosa. Inflorescentia pedunculo ferrugineo-tomentello 2–3 cm longo elata, rachide 7–8 cm longa, ramulis ternatis, verticello primo et interdum secundo foliis ordinariis vel magnitudine aliquantulo redactis suffultis, ramulis aliis pedicellisque ebracteatis; rachis, ramuli pedicellique ut pedunculus ferrugineo-tomentelli. Calyx 5-merus. Corella rubra et fragrans dicta, matura nondum visa. Capsula etiam ignota.

Habitat Amazoniam Brasiliensem.

Brazil: Amazonas; Rio Negro, Preto, Matupiry, Froés 22812, Nov. 1947, type (U); "in open country".

Froés 22812 was distributed by the "Instituto Agronomico do Norte" under the name "*Platycarpum negrense* Ducke", but it is easily distinguishable from that spedies by the ternate instead of opposite, on the upper side scabrid and on the lower softly pubescent leaves and by the somewhat greater length of the hairs by which the various parts of the inflorescence are covered. By its ternate leaves it resembles *Pl. rhododactylum* Woodson et Steyermark, but the latter has a 4-merous calyx and its leaves are on the upper side entirely glabrous and on the lower nearly so, for the very small papillae by which they are covered on this side are seen only by the aid of a lens.

The genus *Henriquezia* has received but little attention in recent years, and the number of its species has increased but slowly. It is now six, the latest addition being *H. macrophylla* Ducke. Below a seventh species will be described, viz. *H. longisepala.*

In this genus too the species are all closely related, and it is therefore difficult to arrange them in natural groups. They are, however, easily distinguishable, and this is mainly due to the following sets of differences, 1) stipules deciduous, i.e. shed shortly after the whorl of leaves to which they belong, begins to expand, or stipules persistent, i.e. shed at the same time as the leaves to which they belong; 2) leaves 5-, 4- or 3-nate; and 3) nerves on the underside of the leaf prominent or not. Less important differences are found in the length of the calyx lobes, in the shape of the leaf and the number of lateral nerves, in the nature of the indumentum, and in the colour the leaves assume in drying. Deciduous stipules are found in *H. verticillata* Spruce ex Bth. with 4- or 5-nate leaves and prominent nerves, in *H. obovata* Spruce ex Bth. with 4-nate leaves of a somewhat different shape but also with prominent nerves, and in *H. oblonga* Spruce ex Bth. with 3-nate leaves and non-prominent nerves; persistent stipules are met with in *H. macrophylla* Ducke with 4-nate leaves and prominent nerves, in *H. Jenmanii* K. Sch. with 3-nate leaves and prominent nerves, the only species with acute, on the underside greyish-tomentellous leaves, in *H. nitida* Spruce ex Bth. with 3-nate leaves and non-prominent nerves, and in *H. longisepala* Brem. also with 3-nate leaves and non-prominent nerves, but differing from *H. nitida,* and in fact from all the other species of which the flowers are known, in the greater length of the calyx lobes, which are nearly as long as the corolla tube, and from *H. nitida* in particular in the ferrugineous-tomentellous inflorescence.

It is not impossible that part of the specimens that have been identified with *H. verticillata* (Froés 21518 et 22784, both from the Rio Negro, Ducke 81, 21683 et 22813, all three from Manaos) will prove to belong to a nearly related, but as yet undescribed species. The leaves of these plants are 4-nate, wider and with a rounded instead of acute base, and provided with a smaller number of nerve pairs (7–9 instead of 11), and the corolla is slightly larger (tube 3 cm long instead of 2.3 cm). However, more material, preferably from the type locality, will have to be compared, before it will be possible to decide whether these differences fall outside the normal range of variability.

My new species offers in this respect no difficulties; the points in which it differs from its allies are numerous and well-marked. Nor can it be doubted that it belongs to the *Henriqueziaceae;* this follows from the presence of the "gland "at the base of the petiole, its slightly zygomorphous corolla with the streak of hairs running down the ventral side of the campanulate throat, the five stamens inserted at unequal height and provided with filaments showing a bent at the base; that it belongs to *Henriquezia* follows from the number and shape of the stipules and their insertion on the basal part of the petiole, the comparatively large size of the corolla, the 5-colpate pollen grains, and the presence of 3 or 4 ovules in each of the ovary cells.

Henriquezia longisepala Brem. n. spec. stipulis persistentibus cum *H. macrophylla* Ducke, *H. Jenmanii* K. Sch. et *H. nitida* Spruce ex Bth., foliis ternatis cum *H. oblonga* Spruce ex Bth., *H. Jenmanii* et *H. nitida*, nervis non prominentibus cum *H. oblonga* et *H. nitida* congruens, a *H. macrophylla* foliis ternatis, multo minoribus et nervis non prominentibus instructis, a *H. Jenmanii* nervis non prominentibus et foliis insuper apice rotundatis, a *H. nitida* inflorescentia ferrugineo-tomentella, a *H. oblonga* stipulis persistentibus et foliis multo minoribus distinguenda, a speciebus omnibus quarum calyx hactenus notus est, insuper longitudine sepalorum diversa.

Arbor parva, circ. 4 m alta. Ramuli novelli obtuse triangulares, ferrugineo-tomentelli, 4–5 mm diam., internodiis 1.0–4.5 cm longis; ramuli veteriores cortice griseo-brunneo opaco vestiti. Folia ternata; petiolus glandula basali excepta ferrugineo-tomentellus 1.5–1.7 cm longus; lamina oblonga vel oblongo-oblanceolata, 12–18 cm longa et 4.5–7.0 cm lata, apice rotundata et mucronulata, basi acuta et in petiolum decurrens, coriacea, utrimque glabra, supra in foliis maturis nitida, sicc. chryseo-lutea, subtus pallidior, costa supra latitudine conspicua, prominula, longitudinaliter striata, subtus prominente, nervis utroque latere costae plerumque 12, utrimque distinguendis sed non prominentibus, inter nervos supra sub lente reticulata, subtus laevis. Stipulae circ. 2 cm longae, acutissime exeuntes, marginibus incurvatae, persistentes. Inflorescentia pedunculo ferrugineo-tomentello 4 cm longo instructa; rachis 3 cm longa, etiam ferrugineo-tomentella. Bracteae ramulos suffulcientes circ. 15 mm longae et 4 mm latae, infimae 3-fidae, aliae integrae, ad anthesin deciduae.

Flores pedicello ferrugineo-tomentello circ. 8 mm longo elati. Ovarium ferrugineo-tomentellum 4 mm altum, utroque loculo ovulis 3 vel 4 instructo. Calycis lobi lineari-lanceolati, 2.5–3.0 cm longi, tertia parte inferiore circ. 3 mm lati, costati, ad medium 6.5 mm lati, tertia parte superiore sensim attenuati, extus ferrugineo-tomentelli, intus griseo-tomentosi. Corolla miniata, extus griseo-tomentosa, tubo campanulato 3.0 cm longo et parte superiore 1.5 cm diam., lobis circ. 1.3 cm longis et 0.9 cm latis. Stamina filamentis glabris 11 et 13 mm longis et antheris 7 mm longis instructa. Granula pollinis depresse globosa, 5-angularia et 5-colpata, 75 μ diam. Discus tomentellus. Stylus glaber 22 mm longus; stigmata 2 linearia 1 mm longa. Capsula nondum visa.

Habitat Amazoniam Brasiliensem.

Brazil: Amazonas; Rio Negro, São Felipe, Igara pé Touri, Froés 28781, 27 Sept. 1952 (ex Inst. Agron. do Norte), type (U).

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OENOTHERA BIENNIS L. VAR. HEMIKLEISTOGAMA, EINE NEUE MUTATION DER O. BIENNIS

TH. J. STOMPS
(Amsterdam)

(*eingegangen am 19. Februar 1957*)

Bekanntlich sind in unserem Lande zwei der Mutationen der *O. biennis* wiederholt wildwachsend gefunden worden, nämlich die *O. biennis* var. *sulfurea* und die *O. biennis* var. *cruciata*. Es ist nun eine dritte hinzugekommen, die bis jetzt in Versuchsgärten noch nicht beobachtet wurde und die ich wegen ihrer Merkmale *hemikleistogama* nennen möchte.

Der Entdecker war Herr Rinke Tolman in Soest (Niederlande). Aus ursprünglich von Kootwijk stammenden Samen blühen in seinem Garten jedes Jahr Hunderte von Exemplaren der *O. biennis*. Im Herbste des Jahres 1951 fiel ihm auf, dass eine Rosette in auffallender Weise von den anderen abwich. Sie lag flach gegen den Boden gedrückt und hatte eine glänzende Kupferfarbe. Und im Jahre 1952 kam daraus ein neuer Typus hervor, schlanker als die *O. biennis*, mit Blättern, die glatter waren als die der *O. biennis*, wo sie buckelig sind, und die hie und da ein rotes Fleckchen oder etwas rötliche Nerven zeigten. Das Hauptmerkmal aber bildeten die kleinen Blüten, von der Grösse einer Hahnenfussblüte, die sich nicht öffneten oder kaum, indem die Kelchzipfel oberhalb der Blüte verbunden blieben. Andere Oenotheren kommen in der Nähe von Soest nicht vor und es handelt sich also sicher um eine neue Mutation.

Im Jahre 1953 hatte Herr Tolman die Freundlichkeit, mir Samen von seiner *O. biennis* und der Mutation, die ich beide 1954 kultiviert habe, zu senden. Der Unterschied war auffallend. Mitte August war die *O. biennis* 1m25 hoch mit dunkelgrünen, buckeligen, 18 × 5 cm messenden Blättern. Die hemikleistogamen Pflanzen hatten uniform einen ganz grünen Stengel, der mitte August bereits 1m45 hoch war und später mehr als 2m erreichte, mit kleineren und grösseren Haaren auf grünen Papillen, dazu flache, gezähnte, hellgrüne, 21 × 5 bis 19 × 4,5 cm messende Blätter mit jetzt weissen Nerven, was wohl durch die anderen Kulturverhältnisse bedingt wurde. Die Knospen waren 5,5 cm lang und grün, nur 6 mm dick, und blieben grösstenteils geschlossen. Einzelne Blüten öffneten sich aber, meistens erst am nächsten Tag, und hatten dann einen Durchschnitt von 2,5 bis 3 cm. Auch die 4 cm × 6 mm messenden Früchte waren immer grün.

Im Jahre 1955 kultivierte ich die beiden Typen aufs neue und auch die beiden reziproken Bastarde. Die Kreuzung *Biennis* × *hemikleistogama*, 60 Individuen an der Zahl, sah der normalen *O. biennis* vollkommen ähnlich, bis auf die Blätter, die glatt und hellgrün waren wie bei der Var. *hemikleistogama*, und erreichte Ende September, wie die *O. biennis*, eine Höhe von 1m50. Die reziproke Kreuzung dagegen, auch 60 Individuen umfassend, war mit Var. *hemikleistogama* identisch, erreichte wie diese eine Höhe von 2m20 und zeigte nur die Blätter der *O. biennis*. Von Kleistogamie war in beiden Kulturen keine Spur zu entdecken.

Nun wurden alle vier Typen geselbstet. Würde die Kleistogamie sich als mendelndes Merkmal erweisen, wie ich es auf Grund einer früheren Erfahrung (STOMPS, 1948) für möglich hielt? Es kam anders! Im vergangenen Sommer erhielt ich vier Kulturen, die denen des vorigen Jahres vollkommen gleich waren, und die Kleistogamie blieb verschwunden.

Die neue Mutation ist interessant im Zusammenhang mit einer Mitteilung BOEDIJN's über eine neue Oenothera-Art, die Baur in der Nähe von Berlin entdeckt und von der er Samen hierher geschickt hatte: die ihm zur Ehre getaufte *O. Bauri* Boed. Diese sieht meiner Var. *hemikleistogama* sehr ähnlich, aber wird gekennzeichnet durch eine rote Anlauffarbe auf Stengeln, Blättern und Knospen und durch stark gedrehte Blätter. BOEDIJN (1924) vermutete schon eine Verwandtschaft mit der *O. biennis* und leitete deshalb die *O. Bauri* von dieser Art ab. RENNER (1956), der die Art, von ihm jetzt *O. hungarica* Borb. genannt, ausführlicher studierte, und viele neue Fundstellen in Ost-Deutschland erwähnte, erklärte sich damit nicht einverstanden und möchte eher eine Beziehung zu der *O. strigosa* (Rydb.) Mackenzie et Busch wahrscheinlich erachten. Nach ihm wird das Merkmal gedrehte Blätter durch die Pollenkörner übertragen, die er deshalb undans nannte, die schlanke Gestalt durch die Eizellen, die laxans genannt wurden. Die *O. Bauri* erwies sich also als heterogam, wie unsere *O. biennis*, bei der ja die Eizellen albicans und die Pollenkörner rubens heissen. Denken wir jetzt noch einmal an das oben erwähnte Kreuzungsresultat! Wenn ich die schlanke Var. *hemikleistogama* mit normalem *Biennis*-Pollen bestäube, so erhalte ich wieder die schlanke Gestalt. Man möchte also folgern, dass bei der Entstehung der Var. *hemikleistogama* eine in laxans mutierte Eizelle der *O. biennis* von einem normalen Pollenkorn befruchtet wurde. Sollte nun bei der Var. *hemikleistogama* auch einmal ein Pollenkorn in undans mutieren, so könnte man vielleicht die *O. Bauri* entstehen sehen, die dann besser *O. biennis* Var. *Bauri* genannt werden würde. Es scheint deshalb empfehlenswert, die Kultur der neuen Varietät im Grossen fortzusetzen.

Zum Schlusse führe ich noch die Diagnose der neuen, hier beschriebenen Varietät an.

Oenothera biennis L. var. *hemikleistogama* nov. var.

Biennis Planta adulta hominis altitudine, vel etiam altior. Caulis viridis, subteres, leviter pilosus, pilis magnitudine variabilibus, partim longioribus, in tuberculo viride positis, partim brevibus, tuberculo basali carentibus. Folia elliptica, leviter dentata, non bullata, pallidae viriditatis, nervo mediano albo, circa 21 cm longa, 5 cm lata. Inflorescentia laxa. Bracteae florum forma foliis radicalibus forma omnino

similes. Gemmae circa 5,5 cm longae, 6 mm crassae, colore viride. Flos flavus, ca 3 cm diametro, rarissime patens, saepe haud apertus, statu clauso decidens. Si aperitur, plerumque interdiu. Stigma in altitudine antherarum apicum. Fructus viridis, ca 4 cm longus, 6 mm crassus.

In horto suo prope Soest, Hollandiae, lecta ab Rinke Tolman, Autumno, anni 1952.

Typus im Herb. Amsterdam.

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THREE NEW FUNGI FROM NORTH AMERICA

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(*received March 15th, 1957*)

In the course of a revision of the genus *Gloeosporium* (VON ARX, 1957), the material by which this genus is represented in the mycological collections of the State College of Washington, Department of Plant Pathology, Pullman (Wash.) has been examined. The author is greatly indebted to Ch. Gardner Shaw for the loan of the specimens. Among those designated as "Gloeosporium spec.", three different species could be recognized, and these seem to be new to science. They are described in this paper.

1. **Monostichella potentillae** v. Arx spec. nov.

Maculae atypicae, 2–7 mm diam., saepe e margine folii ortae, flavo vel griseo-viridulae; acervuli epiphylli, regulariter et dense dispersi vel subgregarii, ambitu orbiculares vel elliptici, 80–140 μ diam., subcuticulares, superne tantum cuticula infuscata, in maturitate irregulariter in lacinias rumpente tecti, tunc late aperti; strato basili omnino plano, 10–15 μ crasso, hyalino vel pellucide brunneo, e cellulis rotundato-angulosis, 2–4 μ metientibus composito; conidiophora atypica, papilliformia; conidia ellipsoidea vel ovoidea-clavata, hyalina, continua, (8-) 14–21 × 5–7 μ.

Hab. in foliis vivis *Potentillae diversifoliae* Lehm., Wyoming, Lookout Sta., Beartooth Lake, Park Co., 20.7.1947, leg. C. L. Hitchcock (16655).

Spots on living leaves, mostly near tip or margin, pale, not sharply margined, 2–7 mm in diameter; acervuli epiphyllous, visible as dark points, scattered or coalescing, round, subcuticular, 80–140 μ in diameter; basal layer 10–15 μ thick, disc-shaped, composed of a pseudo-parenchyma with isodiametric or rounded, rarely elongated, brown cells, reaching 2–3.5 μ in diameter; conidia borne on the upper conical cells of the basal layer, one per cel, elliptical, cylindrical-clavate or reniform, with rounded ends, continuous, hyaline, (8-) 14–21 × 5–7 μ (Fig. 1).

On leaves of *Potentilla diversifolia* Lehm., Wyoming, Lookout Sta., Beartooth Lake, Park Co., July 20, 1947, leg. C. L. Hitchcock (16655).

The species belonging to the genus *Monostichella* v. Höhnel (1916) (Syn.: *Antimanopsis* Petr. 1948) must be considered to be conidial stages of Discomycetes. However the perfect stage of only one species is known. This is *Monostichella salicis* (Westend.) v. Arx (Syn.: *Gloeosporium salicis* Westend.), which is the conidial stage of *Drepanopeziza* *salicis* (Tul.) v. Höhn. (Syn.: *Pseudopeziza salicis* Kleb., viz. KLEBAHN, 1918; NANNFELDT, 1932). *Monostichella* is characterized by the subcuticular position of the acervuli in the host tissue and by the broad elliptical conidia. These are borne on short sterigmata on the upper cells of the basal layer, which consists of a pseudo-parenchyma of rounded or isodiametric cells. In many species of *Monostichella*, the inside of the cuticle above the acervuli is coloured brown by a gummy, skin-like mass.

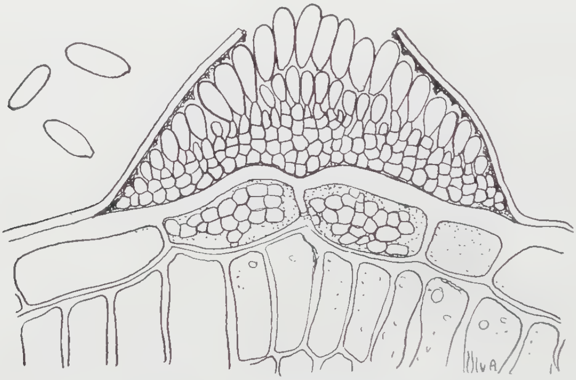

Fig. 1. Vertical section of an acervulus of *Monostichella potentillae*. × 500.

2. **Gloeosporidiella Shawii** v. Arx spec. nov.

Maculae sat atypicae, laxe dispersae, in epiphyllo brunneae vel viridulae, in hypophyllo tantum visibiles, 1–4 mm diam.; acervuli epiphylli, solitarii vel laxe dispersi, in vel sub epidermide evoluti, 40–140 μ diam., primo epidermide pustulatim elevata tecti, ea rupta in maturitate late aperti; strato basili plano, hyalino, ubique 10–13 μ crasso, e cellulis rotundato-angulosis, tenuiter tunicatis, 3–6 μ diam. metientibus composito; conidiophora strati basilis superficiem obtegentia, papilliformia vel conica, hyalina, 9–15 μ longa, 3.5–6 μ crassa; conidia oblongo-fusoidea vel fusoidea-clavata, inaequilatera vel curvula, apice arcuata, postice in papilla attenuata, hyalina, continua, 14–20 × 4–6 μ.

Hab. in foliis vivis *Anaphalis margaritaceae* (L.) Benth. et Hook., Alasca, Red Mountain, Glacier Bay, 12.8.1952, leg. R. Sprague (620).

Spots on living leaves, scattered, round or nearly so, brown to olivegreen, 1–4 mm in diameter; acervuli epiphyllous, intra- or subepidermal, colourless, round or irregular, 40–150 μ in diameter; basal layer 10–13 μ thick, discoid, composed of a pseudo-parenchyma with isodiametric or rounded, hyaline cells that are 3–6 μ in diameter; conidiophores densely crowded, short cylindrical or conical, hyaline, 9–16 × 3.5–6 μ, with acrogenous conidia; conidia elliptical, clavate or broadly fusiform, slightly curved, apically arcuate or beaked, continuous, hyaline, 14–20 × 4–6 μ (Fig. 2*a*).

On leaves of *Anaphalis margaritacea* (L.) Benth. et Hook., Alaska, Red Mountain, Glacier Bay, August 12, 1952, leg. R. Sprague (620).

The type species of the genus *Gloeosporidiella* Petr. is *Gloeosporium ribis* (Lib.) Mont. et Desm. = *Gloeosporidiella ribis* (Lib.) Petr. This fungus is the conidial stage of *Drepanopeziza ribis* (Lib.) v. Höhn. (Klebahn, 1918). According to the description of Petrak (1921), the conidia are produced directly on the cells of the basal layer. Examination of a number of specimens showed that the conidia may indeed be borne on the short conical upper cells of the basal layer. Often, however, these conidiophorous cells are longer and more or less cylindrical like true conidiophores.

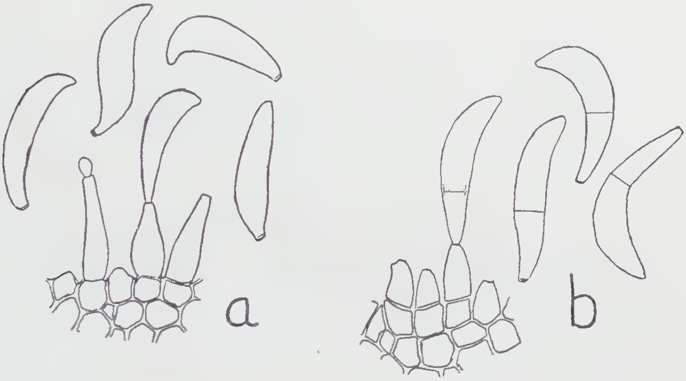

Fig. 2. Conidiophores and conidia of a. *Gloeosporidiella Shawii*, b. *Marssonina saxifragae*. × 500.

Characteristic of the members of the genus *Gloeosporidiella* are the acervuli, which are seated in or beneath the epidermis of the host plant and are light-coloured or colourless. The conidia of all the species are elliptical clavate, broadest in the upper third part, curved, especially near the apex and beaked. This genus is closely related to *Marssonina* Magn. The only difference is that the conidia of the latter genus are septate. *Gloeosporidiella* is also related to *Cryptocline* Petr. (Syn.: *Gloeotrochila* Petr.). In this genus, the conidia are round, oval or elliptical and not beaked, and they are produced acrogenously on cylindrical or thread-like conidiophores.

3. **Marssonina saxifragae** v. Arx spec. nov.

Maculae irregulariter laxe vel dense dispersae, plerumque accuratae, 1–3 mm diam.; acervuli semper epiphylli, solitarii, in vel sub epidermide evoluti, primo epidermide tecti, ea rupta in maturitate, plus minusve late aperti; strato basili ubique 7–15 μ crasso, plano vel parum concavo, hyalino, e cellulis rotundato-angulosis, 3–4 μ diam. metientibus composito; conidiophora strati basilis superficiem obtegentia, papilliformia, conoidea vel lagenaria, hyalina, 5–12 μ longa, 3–4 μ crassa; conidia oblongo-fusoidea vel fusoidea-clavata, curvula, infra media obscure septata, apice arcuata, postice in papillam attenuata, 17–26 × 5–7 μ.

Hab. in foliis vivis *Saxifragae mertensianae* Bong., Washington, Wahkiakum, Cathlamet, 4.1907, leg. A. S. Doster.

Spots on living leaves, necrotic, pale or greyish, round or nearly so, 1–3 mm in diameter; acervuli epiphyllous, one in the central area of the lesion, subepidermal, discoid or saucer-shaped, rupturing the covering epidermal cells; basal layer hyaline, 7–15 μ thick, composed of an incomplete pseudo-parenchyma with isodiametric, rounded or elongated cells, about 3–4 μ in diameter, with thin and hyaline walls; conidiophorous cells conical, blunt, 5–12 μ long and 3–4 μ broad, acrogenously producing conidia; conidia fusiform, lunate, curved, especially in the upper third part, pointed or beaked, with an indistinct septation in the lower third part, hyaline, 17–26 × 5–7 μ (Fig. 2*b*).

On leaves of *Saxifraga mertensiana* Bong., Washington, Wahkiakum, Cathlamet, along wet rocky bluffs, April 1907, leg. A. S. Doster.

M. populi (Lib.) Magn., the type species of the genus *Marssonina* Magnus (1906) is identical with *Gloeosporium castagnei* Desm. et Mont., which is the type species of the genus *Gloeosporium* Desm. et Mont. (1949) (von Höhnel, 1916). Therefore the name *Marssonina* is a typonym of *Gloeosporium*, but as it would not be advisable to reintroduce that name, *Marssonina* is proposed for conservation.

Several *Marssonina* species are known to be the conidial stage of Discomycetes, especially of *Drepanopeziza* and *Diplocarpon* species (Nannfeldt, 1932). The genera *Monostichella*, *Gloeosporidiella*, *Marssonina*, *Cryptocline*, *Fusamen* Karst. (Syn.: *Calogloeum* Syd., *Platycarpium* Karst.), *Cryptosporiopsis* Bub. et Kab. (Syn.: *Myxosporium* auct. non Link, *Discosporium* v. Höhn. and others), *Phlyctaena* Mont. et Desm. (Syn.: *Allantozythia* v. Höhn.) and *Cryptomycella* v. Höhn. are related, and they too must be regarded as conidial stages of Discomycetes.

It is known that other genera of the Melanconiales are conidial stages of Pyrenomycetes, especially of Diaporthaceae (including Gnomoniaceae). These genera are built up according to the Phomopsis type. The conidia are more or less fusiform, guttulate and are borne apically on linear or subulate, pointed and densely crowded conidiophores. Typical members of this group are such genera as *Discula* Sacc. (Syn.: *Gloeosporidium* v. Höhn.), *Marssoniella* v. Höhn. or *Discella* Berk. et Br. (Syn.: *Septomyxa* Sacc.).

Some species described in *Marssonina* are to be excluded, and should be placed in the Phomopsideae, especially in the genus *Discella*. Typical members of the latter genus are for example *Marssonina Tulasnei* (Sacc.) Died. on *Acer*, *M. quercina* (Wint.) Lentz or *M. ochroleuca* (Berk. et Curt.) Lentz on *Castanea* (Lentz, 1950). The fructifications of these species may be either melanconoid or pseudopycnidial. *Marssonina juglandis* (Lib.) Magn. = *Marssoniella juglandis* (Lib.) v. Höhn. is the type species of the genus *Marssoniella*. This species is characterized by the subcuticular position of the acervuli.

SUMMARY

Among the Gloeosporium material received from the herbarium of the State College of Washington, Pullman, three specimens were found which proved to represent undescribed species. They are here described under the names *Monostichella potentillae*, *Gloeosporidiella Shawii* and *Marssonina saxifragae*. Further the taxonomy and the nomenclature of some genera belonging to the Melanconiales are briefly discussed.

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DISTICHOUS AND PSEUDODISTICHOUS MOSSES

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(Groningen)

(received March 11th, 1957)

In revising the family *Phyllogoniaceae* for the Flora Malesiana, I found that in many species which so far were included in this family, the leaves are, contrary to expectation not distichously disposed. As that type of phyllotaxis is regarded as the main diagnostic character of the family, it was a surprise to me that other bryologists had not noticed this fact. For this reason I have paid special attention to the phyllotaxis of the species belonging to the *Phyllogoniaceae*.

In Brotherus, Natürl. Pflanzf. ed. 2, 11 (1925) 175, the family includes three genera, viz. *Phyllogonium* Brid., *Orthorrhynchium* Reichdt. and *Eucatagonium* (Broth.) Fleisch. The first genus, *Phyllogonium*, comprises, as far as I could check, distichophyllous species only (Fig. 5*a*). The leaves are inserted alternately on the complanate branches, the distances between the consecutive leaves in both rows being equal. The genus is restricted to S. America and Africa (Congo), and is characterized by the well-marked alar cells and by the strongly ampliate leaf bases.

The last-mentioned genus, *Eucatagonium*, also occurs in S. America, and further in Africa and Australia. In 1922 Fleischer transferred the genus to the family *Phyllogoniaceae*. Before this change it was regarded as a subgenus of *Catagonium* C. Muell., a genus belonging to the *Plagiotheciaceae;* this family includes several complanate mosses. Fig. 5*b* shows two branches of *Eucatagonium politum* (Hook. f. et Wils.) Broth. At first sight it is clear that the phyllotaxis is totally different from that in *Phyllogonium:* the leaves are not regularly arranged in two rows. However, these irregularities are easily overlooked. As a matter of fact, Fig. 3, which is a copy of fig. 565 of Brotherus, Natürl. Pflanzf. ed. 2, 11 (1925) 176, does not show them. In comparing figures 5*b* and 3 one undoubtedly sees the difference: in Fig. 3 the distances between the consecutive leaves on each side of the stem are equal, whereas in Fig. 5*b* they are unequal and even the alternation is not always regular.

If in Fig. 5*b* the leaves are not distichously disposed, what then is the phyllotaxis? To answer this question I have attempted to determine what the result would be, if a radially symmetric stem with a phyllotaxis belonging to the so-called main series is compressed. The main series in phyllotaxis is formed by the Fibonacci numbers 1, 2, 3, 5, 8, 13, 21 etc., in which any term is the sum of the two preceding terms. Each term indicates the number of contact parastichies and simultaneously the possible number of orthostichies Schoute's

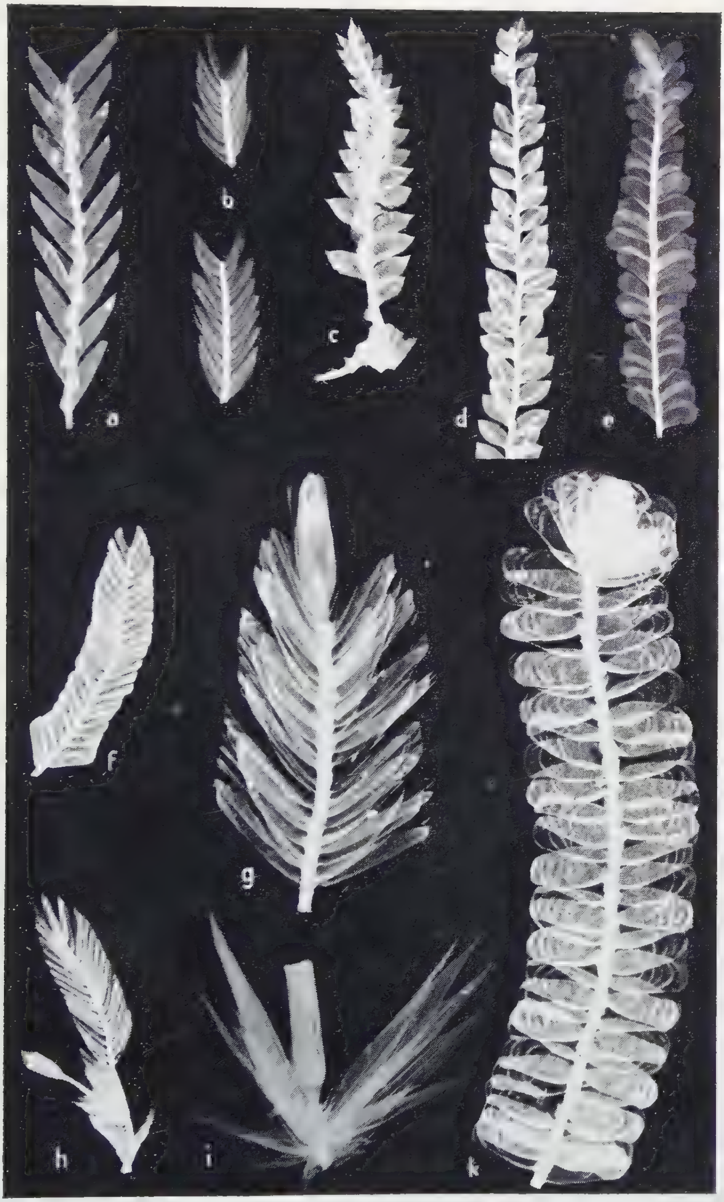

Fig. 5. Stems and in h. and i. capsules of different mosses (× 6). a. *Phyllogonium serra*. b. *Eucatagonium politum*. c. *Cyathophorella hookeriana*. d. *Thamnium ellipticum*. e. *Homaliodendron beccarianum*. f. *Orthorrhynchium elegans*. g. *Orthorrhynchium philippinense*. h. Capsule of *O. elegans*. i. Capsule of *O. philippinense*. k. *Neckeropsis lepineana*.

investigations have shown that it are these numbers of parastichies, and no others, which nearly always occur in higher plants. Alexander Braun, observing the divergences in phyllotaxis at a much earlier

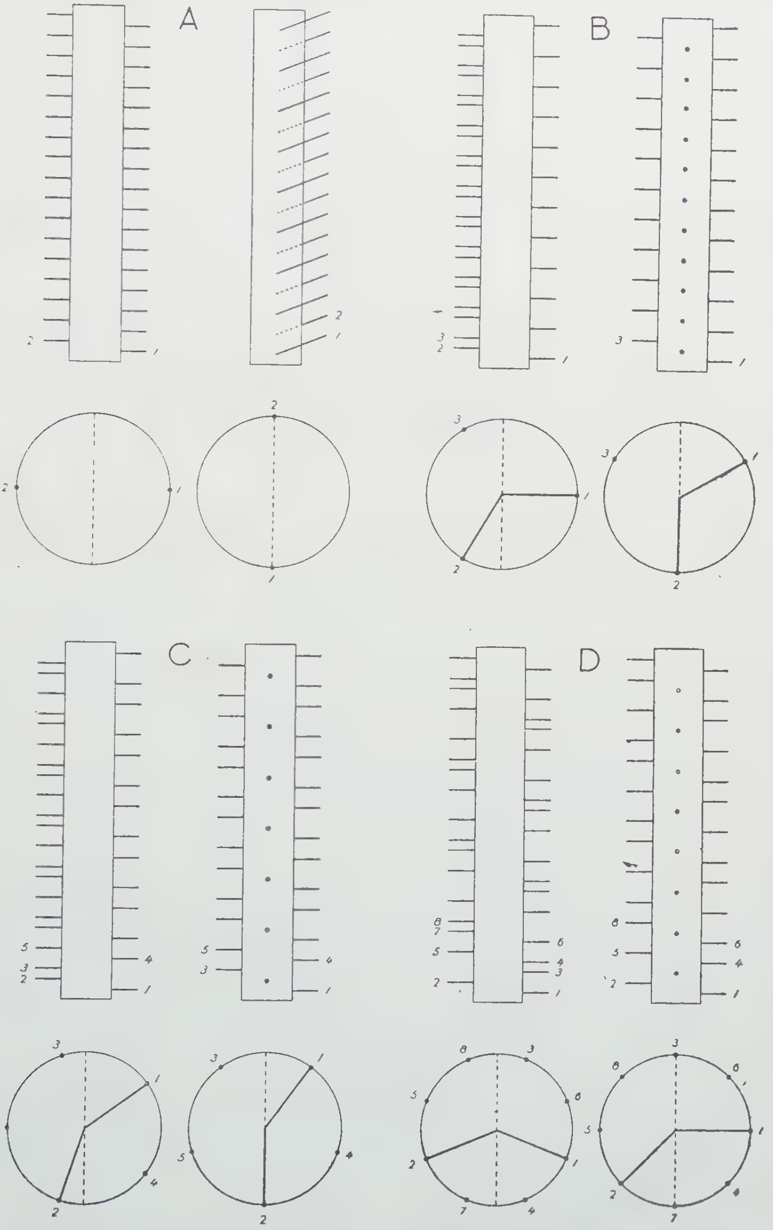

Fig. 1. Phyllotaxis with 2 (A), 3 (B), 5 (C), or 8 (D) orthostichies on complanate stems. The figures on the left relate to stems without median leaves, the figures on the right to those with either one or two rows of median leaves.

date, found the same numbers of orthostichies in the greater part of the mosses.

Fig. 1 demonstrates what will happen if the number of orthostichies is respectively 2, 3, 5 or 8, when the radially symmetric stem becomes a complanate one: the leaves, so far as they are found on different sides of the median line, are then shifted either to the left or to the right.

a. Leaves disposed in two orthostichies. (Fig. 1A). The leaves are distichously inserted, as is seen in *Phyllogonium* (Fig. 5*a*). However, there is a second possibility, *viz.* if the leaves are inserted in the median line; in the complanate stem the leaves are then found on the dorsal and the ventral side. This case with all the leaves pointing in one direction, is often realized in *Rhizogonium novae-hollandiae* Brid.

b. Leaves disposed in three orthostichies (Fig. 1B). In this case the number of leaves on one side of the median line may become twice as large as that on the other side. I did not find this type of phyllotaxis in complanate mosses. However, the other possibility *viz.* that one of these orthostichies is found in the median line, is realized in several mosses. Fig. 5*c*. shows the two rows of lateral leaves and the single row of ventral median leaves (amphigastria) in *Cyathophorella hookeriana* (Griff.) Fleisch.

c. Leaves disposed in five orthostichies. (Fig. 1C). Let us first consider the transitional case, *i.e.* that with one orthostichy in the median line. The lateral leaves are apparently disposed in two rows, and in each row the distances between the consecutive leaves are in the ratio 2:3:2:3 etc. If none of the five orthostichies is in the median line, the distances between the consecutive leaves on one side would be in the ratio 1:2:1:2, on the other side 2:3:2:3. Neither arrangement agrees with Fig. 5*b* of *Eucatagonium*, nor did I discover this arrangement in any other complanate moss.

d. Leaves disposed in eight orthostichies. In the transitional case there are two rows of median leaves, a dorsal and a ventral one (Fig. 1D to the right). If leaf number 1 is ventrally inserted, then leaf number 5 is dorsally placed, and on both sides the ratio of the distances between the consecutive leaves is 2:3:2:3. If median leaves are absent, the ratio of the distances between the consecutive leaves is on both sides 1:2:3:2:1 etc. This very characteristic ratio varies on the two sides in this way that if on one side it is 1:2:3:2:1 etc. it is on the other side 3:2:1:2:3 etc. If we measure in Fig. 5*b* of *Eucatagonium* the distances between the consecutive leaves on either side, then we find that the ratio is indeed 1:2:3:2:1 etc., and if on one side of the stem two leaves are near to each other, there is a large gap between the two leaves on the opposite side. My conclusion therefore is that the leaves of *Eucatagonium* are not really distichous, but that they are arranged in eight orthostichies. For this reason we will call them pseudodistichous.

That this arrangement is also present in the genus *Catagonium* and in other genera of the *Plagiotheciaceae*, may be taken as an indication that *Eucatagonium* is closely allied to *Catagonium*, of which it was originally regarded as a subgenus. There are other reasons for assuming a close relation between the two genera: the leaf cells in *Eucatagonium* are thin-walled and long-linear just as in *Catagonium*, whereas in *Phyllogonium* the leaf cells have incrassate and pitted walls, and are much shorter linear to rhombic. The capsule of *Eucatagonium* is borne on a well-developed seta, whereas in *Phyllogonium* the seta is short or absent. In my opinion, Fleischer who was not aware of the pseudodistichous leaves, made a mistake in transferring the (sub-) genus *Eucatagonium* to the *Phyllogoniaceae;* its correct place is near the genus *Catagonium* in the *Plagiotheciaceae.*

For the sake of completeness I wish to add that it is not necessary to accept precisely 8 orthostichies, for with 13 or 21 (the next Fibonacci numbers of the main series) orthostichies too we arrive at a disposition which agrees with the observation. The differences between the dispositions obtained in the case of 8 and 13 orthostichies are very small indeed. To demonstrate the comparatively small size of these differences I have given in Fig. 2 the situation in the case of a phyllotaxis with the limiting angle of the main series, the so-called Fibonacci angle, *i.e.* 137° 29′. The resulting disposition in a complanate stem is in that case nearly the same as the one we arrive at with an angle of 135° (*i.e.* with 8 orthostichies), at least if we confine our attention to a short part of the stem. Only if a much longer part of the stem is considered, we observe a slight deviation of the ratio mentioned above, *viz.* 1:2:3:2:1. Our final conclusion is this: if the arrangement remains regular along the whole length of the branch, the leaves are disposed in 8 orthostichies, but if there is a slight shifting, we have a closer approximation to the limiting angle

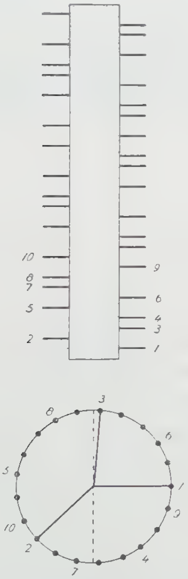

Fig. 2. Phyllotaxis without orthostichies, the divergence between the consecutive leaves is 137° 29′, the Fibonacci angle.

of the main series. In this case it is not possible to determine whether the number of orthostichies is 13, 21, 34 or even higher.

Further study of the phyllotaxis in complanate mosses has shown that pseudodistichous leaves, *i.e.* leaves that are in reality in 8 or more rows, occur in several families, especially in the *Neckeraceae* and the *Plagiotheciaceae* (see Fig. 5*d Thamnium ellipticum* (Bosch et Lac.) Kindb. and Fig. 5*e Homaliodendron beccarianum* (Hamp.) Broth.).

Let us now consider the third genus, *Orthorrhynchium*, which occurs in the Malaysian region. In the herbaria several specimens have been named *O. philippinense* C. Muell., but a re-examination clearly showed that two different species have been included under this name. The leaves of the first moss (Fig. 5*f*) proved to be perfectly distichous, but this moss is incorrectly referred to *O. philippinense* C. Muell.; it is in reality *O. elegans* (Hook. f. et Wils.) Reichdt. which was originally described from Australia. *O. beccari* C. Muell. from New Guinea is also the same species.

The other *Orthorrhynchium* specimens, included under the name *O. philippinense* C. Muell. are totally different (Fig. 5*h*). They are pseudodistichous, *i.e.* the leaves are arranged in 8 or more rows. The question is now whether this moss really belongs to *Orthorrhynchium*. The phyllotaxis seems to make this improbable. In search for other discrepancies, I turned my attention to the capsule of this *Orthorrhynchium* species which hitherto was unknown. However, the specimen collected by Carr (no 11944) in New Guinea proved to bear capsules. The seta is short or nearly absent, and the capsule itself is long and cylindrical (Fig. 5*i*). The capsule of *O. elegans* (Fig. 5*g*) has a well developed but short seta and is ovoid. In my opinion these two points of difference (the difference in phyllotaxis and that in shape and development of the capsule) sufficiently prove that this part of *O. philippinense* C. Muell. will have to be removed from the genus *Orthorrhynchium*. But to what other genus should we transfer the species? Now in Journ. of Bot. 43 (1905) 342 A. and E.S. Gepp recognized that *O. philippinense* C. Muell. from the Philippine Islands and *Neckera*

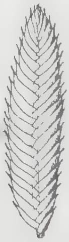

Fig. 3. *Eucatagonium politum* (fig. 565 from Brotherus, Natürl. Pflanzf. ed. 2, 11).

phyllogonioides Sull. from Luzon are conspecific. It is for this reason that in BARTRAM's Mosses of the Philippines (1938) 232 this species is named *O. phyllogonioides* (Sull.) E. G. Britt. ex Bartr. To my opinion it is better to transfer this part of *O. philippinense* C. Muell. for the present to the genus *Neckera* and to accept for the species the name *Neckera phyllogonioides* Sull.

Let us wind up with a few remarks on another dilemma. In a key to the genera of the *Neckeraceae* one finds:

1. Leaves in 4 rows......*Homaliodendron, Neckeropsis.*
2. Leaves in 8 rows......*Neckera, Himantocladium.*

The arrangement of the leaves in 8 rows is easily recognizable; there may be some difficulty only if a few leaves are not directed laterally, but an arrangement in 4 rows did not agree with the theory of phyllotaxis. There are two possibilities; either there are 4 rows, and then the phyllotaxis is of the first accessory series 1, 3, 4, 7, 11, etc., or the 4 rows do not really exist. To solve this problem, I have calculated the disposition of the leaves in the case of 4 orthostichies (Fig. 4A) and in that of 7 orthostichies (Fig. 4B). The ratio of the distances between consecutive leaves is 1:3:1:3 or 1:3:3:1 and 1:2:1:3:1 etc. respectively. Neither of these dispositions occur in *Neckeropsis* (Fig. 5*k*), but our figure clearly shows that the ratio is the same as in Fig. 5*b*, which relates to *Eucatagonium.* The conclusion in this case is also that the arrangement in 4 rows is a fiction; the

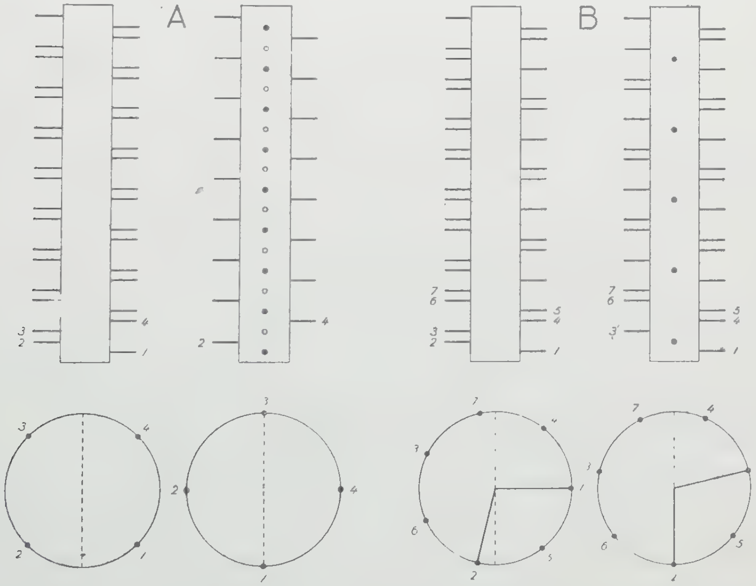

Fig. 4. Phyllotaxis with 4 (A) or 7 (B) orthostichies on complanate stems.

moss is not tetrastichous, but pseudo-tetrastichous; in reality it is octostichous.

The above considerations may serve to show that in mosses a morphological study of the phyllotaxis may refrain us from drawing false taxonomic conclusions and that at least in some moss families the phyllotaxis may be of taxonomic importance.

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A NEW PEPEROMIA, COLLECTED BY THE SURINAME EXPEDITION 1948/1949

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(*received July 11th, 1957*)

Peperomia lanjouwii Yuncker n. sp.

Herba parva delicata subcaespitosa repens, caule pergracili sat conferte piloso, pilis erectis; foliis alternis vel supremis oppositis elliptico-obovatis, apice rotundatis, basi acutis vel subobtusis, supra crispo-pubescentibus subtus glabris vel dissite pubescentibus ciliolatis palmatim 3-5-nerviis; petiolo pergracili; spicis terminalibus axillaribusve gracillimis; drupa obliquo-ovoidea, apice obliqua, stigmate subapicali.

A very small, delicate, subcespitose, herbaceous plant, the stems scarcely 1 mm. in diameter when dry, pilose with spreading hairs, commonly densely so in young growth, branching, the sterile branches comparatively short and stolon-like, the fruiting branches ascending 3–5 cm. Leaves alternate, or the uppermost appearing opposite, the blades elliptic-obovate, the apex rounded, the base acute or obtusish, up to 7 mm. wide and 10 mm. long, but mostly about 3–4 × 5–7 mm., the upper surface crisp-pilose, the lower surface glabrous, or occasional leaves pilose, the margin ciliate, palmately 3- or 5-nerved, the nerves with very slender cross-connecting-anastomosing nervules as viewed by transmitted light, drying membranous and translucent, the blades with a pair of longitudinal brown stripes above and pale green beneath when growing; petiole filiform, mostly 3–5 mm. long, sparsely pilose glabrescent, flattened above and laterally ridged by the decurrent blade margins. Spikes terminal or axillary, very slender, closely flowered, up to 1.5 (or more?) cm. long, the peduncle 5–8 mm. long, thinly pilose glabrescent, the bracts round-peltate, the margin uneven or irregular. Fruit obliquely ovoid with oblique apex and subapical stigma.

Distribution: Known only from Suriname.

Suriname, Nassau Mts., in forest on dead tree trunk near km 7.5, Mar. 11, 1949, J. Lanjouw and J. C. Lindeman n. 2598, type, in herb. Utrecht. The following specimens are fragmentary. They cannot be reconciled with any other species and sufficiently resemble the above cited specimen to warrant including them on a tentative basis: Rikanau, near Moengo (Lindeman n. 5991); Suriname River, Jodensavanne-Mapane Creek area (Lindeman n. 4986); Nassau Mts. Lanjouw & Lindeman n. 2427A; n. 2632; n. 2670; n. 2933).

This species appears to be a member of a group including several South American species characterized by slender, more or less stoloniferous stems, small leaves and small spikes, of which *P. rotundifolia* is the commonest and most wide-spread. It seems to be most closely related to *P. rotundifolia* and to *P. tafelbergensis*. It differs from both in the shape of the leaves, shorter stolons, and with brown or purple stripes on the upper side of the blade. It also bears some resemblance to *P. obovalis* of Colombia. That species, however, differs in having crisp-puberulent stems, somewhat larger glabrous leaves, and longer spikes. From *P. arenillensis* of Ecuador, which also has purple-striped leaves, it differs in having the lower blade surface glabrous, shorter spikes, etc. The presence of the brown (or purple) stripes on the leaves, the glabrous lower blade surface, and the short stolons are distinctive features. It is named for the senior collector.

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THE INFLUENCE OF LIGHT QUALITY ON THE FLOWERING RESPONSE OF SALVIA OCCIDENTALIS

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(*received May 10th, 1957*)

INTRODUCTION

It has been found that an irradiation of low light intensity, supplementarily given to a short light period of high intensity (photoperiod or main light period), has a day lengthening effect on several plants. RASUMOV (1933) found that the red part of the spectrum has the greatest activity in this supplementary light reaction. Similar results were obtained by WITHROW *et al.* (1934, 1936 a and b), WASSINK *et al.* (1950, 1951) and by STOLWIJK (1952, 1954).

The same photoperiodic effect can be achieved when this period of supplementary light of low intensity is replaced by a "night break" i.e. an interruption of the dark period by a short irradiation of high light intensity.

The action spectrum of this night break reaction has been found to be similar for both long day and short day plants (PARKER *et al.*, 1946, 1950; BORTHWICK *et al.*, 1948).

A maximum of activity has been found in the red region of the spectrum with a second, smaller maximum in the blue part. Moreover it has been found by BORTHWICK *et al.* (1952) that the effect of a red light flash can be reversed by an infra-red irradiation.

Not very much is known about the influence of the main light period on photoperiodic effects.

HAMNER (1940) found that already one long dark period induces flowering in *Xanthium pennsylvanicum*, provided there is a light period of high intensity preceding the inducing long dark period. Whereas this light period can be substituted by a sugar treatment, BONNER *et al.* (1953) concluded that this light period is only necessary to produce photosynthates.

DE ZEEUW (1953) obtained flowering of *Perilla*, a short day plant, in 18 hrs light per day and even in continuous light, provided the plants were kept in light of a low intensity.

Only a few indications can be found on the influence of the light quality of the photoperiod on flowering.

ODÉN (1929) states that light of short wave lengths promotes heading of lettuce, whereas light of long wave lengths promotes flowering and fruiting.

Kleshnin (1950) could confirm this conclusion for lettuce, as well as for some other long day plants and for a short day plant, *Amaranthus retroflexus*.

Popp (1926) found that *Petunia* and *Mirabilis* did not flower in daylight from which the shorter wave lengths were filtered out, whereas flowering occurred in white light of the same intensity.

Wallrabe (1943) working with *Kalanchoë Blossfeldiana*, a short day plant, came to the conclusion that a short day treatment in blue light is more effective than the same treatment in red light. In a short day in green light no flower initiation occurred at all.

Stolwijk *et al.* (1955) growing *Hyoscyamus niger* in light of different spectral regions, concluded that this plant needs violet, blue or infra-red during the main light period to obtain flowering. A long day however is necessary.

In this paper experiments are described which show the same blue or infra-red necessity for inducing the long day effect on the short day plant *Salvia occidentalis*.

Methods and Material

In the following experiments "white" light and light of three different spectral regions have been used to grow plants: red, green and blue light.

The plant growth chambers in which the experiments were carried out under exclusion of daylight have been described by Van der Veen (1950). The light was obtained by using different coloured fluorescent tubes (Philips) from which the undesired part of the spectrum was filtered out by suitable filters of "Plexiglas" (Röhm & Haas). The "TL"33 fluorescent lamp has been the light source for the experiments in "white" light. Red light was obtained by using a combination of the "TL" lamp no 103647 and the filter "Rot 1" (Fig. 1a.).

The "green" light, emitted by "TL" 17 lamps is purified by using the filter "Gelb 3" which cuts of all radiation with a wave length < 4700 Å (Fig. 1b).

Two different types of blue light were used. For both the light source was the same "TL" fluorescent tube, no. 103648, the filters however were different. One of them "Blau 27 alt" has only a transmission in the blue part of the spectrum, whereas the other one "Blau 27 neu", with a somewhat different transmission characteristic in the blue region, still has a transmission in the infra-red part. The pure blue light without infra-red contamination will be referred to as blue, the impure form (with infra-red) as blue + i.r. (Fig. 1c and d). In some experiments infra-red radiation was added by using incandescent light (100 Watt bulbs) from which the visible part of the spectrum ($\lambda < 7000$ Å) was filtered out by using a combination of the filters "Rot 1" and "Blau 27 neu". Light intensities were measured in $\mu W/cm^2$. The amount of added infra-red is given for the region 7000–8000 Å.

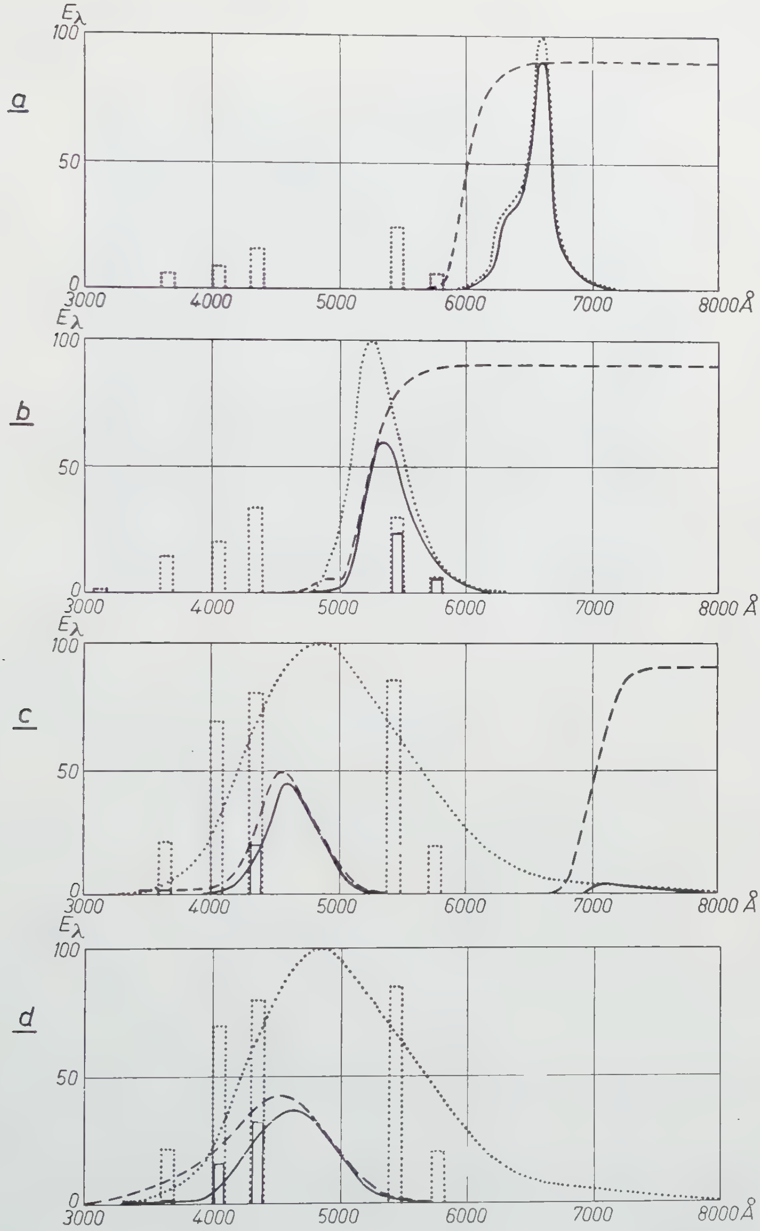

Fig. 1. The relative spectral energy distribution of the filtered light (solid line). a: red light; b: green light; c: blue light + infra-red; d: blue light. The emission curve of the fluorescent tubes is given by the dotted line, the transmission curve of the filters by the broken line.

As far as known *Salvia occidentalis* has never been used before in daylength experiments. Since several years a clone is cultivated by growing cuttings under long day circumstances. It has been proved to be an obligate short day plant.

Experimental data

1. *Day length experiments in white light*

These experiments were carried out in white fluorescent light ("TL" 33) in 3 different day lengths: 10 hrs, 16 hrs and 24 hrs light per day with a light intensity of 1100 μW/cm^2. In short days plants were flowering after some time. In 16 hrs and 24 hrs light per day plants remained vegetative.

The first macroscopic sign of the reproductive stage appears when instead of a young leaf pair, the tips of a bushel of bracts are visible.

By varying the length of the short day treatment, the flower induction can be influenced quantitatively. A slight induction is obtained by a treatment of 14 short days after which the plants are grown under long day circumstances. This induction period gives rise to a development of some bractlike leaves. However, no inflorescence with flower primordia is formed and the formation of normal leaves is continued. An induction period of 21 short days is sufficient for the formation of the inflorescence, although its development into flowering is inhibited by the following long days. Vegetative development starts again after laterals have been grown from the axils of the highest leaf pair. The same development is obtained after an induction period of 28 short days. When the plants were left in short days, flowering occurred 49 days after the beginning of the treatment.

Laterals are more sensitive to an induction period than the main stem. After 14 short days the apices of the laterals were already induced to form inflorescences.

In the following experiments the growing points were not dissected after a special treatment, but afterwards the plants were grown for some time in long day circumstances. In this way even the above mentioned slight effect of a short induction period could be noticed.

By using stronger light sources a much higher light intensity was obtained. (3500 μW/cm^2). This intensity however seemed to be too high for favourable growth of *Salvia occidentalis*. In a long day, stems are growing diageotropically, smaller leaves are formed, and the anthocyanin formation is stimulated, whereas especially the older leaves show a marked epinastic curvature (Fig. 2). In the experiments described in the next chapter it was found that the diageotropic growth is caused by the red part of the spectrum. To find out the most favourable light intensity, plants were grown in four different light intensities which were obtained in one plant growth chamber by using gauze filters. The intensities used are 2500, 1250, 850 and 250 μW/cm^2. The higher the light intensity, the more pronounced are the symptoms described above. It is remarkable that in the lowest light intensity plants entered into the reproductive phase although a long day of 16 hrs light per day was given.

The tips of the bracts appeared 30 days after the beginning of the treatment and after 55 days these plants were flowering. The plants grown in the other intensities remained vegetative throughout this time (Fig. 2).

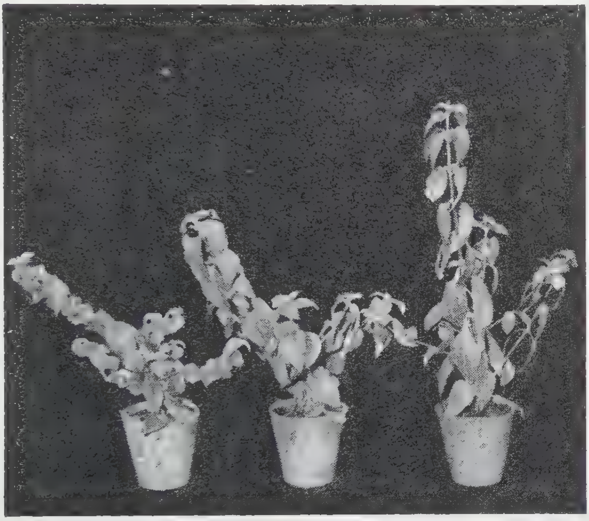

Fig. 2. The influence of the light intensity of the main light period on the photoperiodic effect of a long day treatment on *Salvia occidentalis*. From left to right: plants grown in 16 hrs of light per day with a light intensity of 2500, 850 and 250 μW/cm^2. 39 days after the beginning of the treatment. The plant grown under 250 μW/cm^2 shows inflorescences.

2. *Influence of light quality of the main light period*

In order to investigate the influence of light of different spectral regions on length growth, plants were grown in red, green, blue and blue + infra-red light.

It has been found that the elongation of internodes of different plants, grown in blue light is stimulated when the infra-red part of the spectrum, emitted by the fluorescent tubes, is not filtered out (Fig. 3).

This stimulation is entirely due to the infra-red contamination and not to differences in the blue region of the spectrum (fig. 1c and d). The same effect was obtained when plants were grown in blue light (fig. 1d) to which infra-red was added.

Next to this effect on elongation the apical dominance is influenced by infra-red irradiation. The development of the laterals which are normally formed is more or less inhibited when grown in blue + infra-red (Fig. 3).

The most remarkable effect however is the flowering response of *Salvia*, grown in a long day (16 hrs light per day) in light of different spectral regions.

Decapitated plants were grown in short day (10 hrs) and long day (16 hrs) during 32 days. The light intensities in quanta were equal. The observations were made on the laterals growing from the axils of the highest leaf pair after decapitation. After the treatment plants were kept in a glasshouse under normal long days. The last observations were made 77 days after the beginning of the treatment. The results are given in Table I. No difference was obtained in response to a short day treatment in red and in blue light. The number of leaves formed up to the inflorescences was the same (5 leaf pairs). Plants treated with long days in blue and blue + infra-red remained vegetative for the whole time.

Although in green light a long day was given, the flowering response of this lot of plants was the same as the plants exposed to short days in blue and red light. The bracts became macroscopically visible after the same time and the same number of leaves up to the inflorescence was formed.

The plants showed about a similar reaction when treated with a long day in red light. Flower formation was obtained but it was somewhat retarded as compared to the other flowering groupes. In red light 8 pairs of leaves were developed before flower initiation occurred.

Already 3 days after the beginning of the treatment in red light leaves are showing a marked epinastic curvature. This curvature was less visible in the newly formed leaves. The size of the last ones is smaller than the size of the comparable leaves from the other light treatments. The diageotropical growth already mentioned above is only found in plants grown in red light. In other experiments light intensities were used as high as possible and by means of gauze filters 4 different light intensities could be obtained. The plants were exposed during 4 weeks to 16 hrs of red, blue and blue + infra-red light per day of different intensities (table 2). After this treatment

TABLE I

The response of *Salvia occidentalis* to a short day and a long day treatment in different spectral regions (equal amounts of quanta). Duration of the treatment 32 days. Day temperature 22° C. Night temperature 17° C.

Spectral region	intensity (μW/cm^2)	daylength hrs per day	condition of the apex	number of leaf pairs up to the inflorescence
blue	600	10	generative	5
red	370	10	generative	5
blue	600	16	vegetative	> 10
blue + i.r.	600	16	vegetative	> 11
green	500	16	generative	5
red	370	16	generative	8

plants were kept under long day circumstances in white light during another 6 weeks.

As can be seen in Table II even in the lowest blue light intensity used, 90 μW/cm^2, no flowering occurs. In red light however the lowest light intensity used, 360 μW/cm^2, gave rise to flower initiation.

TABLE II

The flowering response of *Salvia occidentalis* to a long day treatment in different intensities of blue, blue + i.r. and red light. Duration of the treatment 28 days. Day temperature 22° C. Night temperature 17° C.

Condition of the growing point												
Spectral region	light intensity in μW/cm^2											
16 hrs. day	75	90	250	300	360	375	420	750	880	1200	1800	3600
blue		veg.		veg.			veg.		veg.			
blue + i.r.	veg.		veg.			veg.		veg.				
red					gen.					veg.	veg.	veg.

In the higher intensities of red light, the plants remained vegetative. Representative plants grown in light of an intensity of 900 μW/cm^2 are shown in Fig. 3.

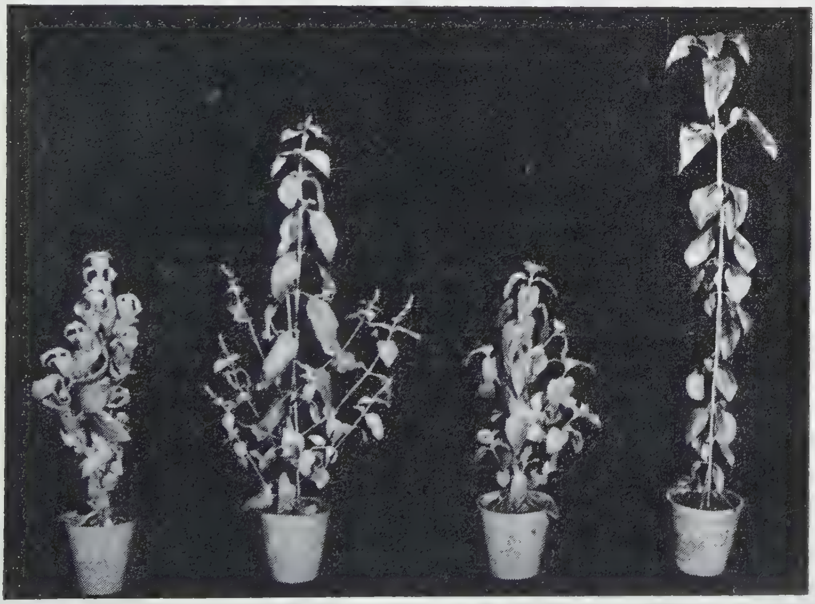

Fig. 3. The response of *Salvia occidentalis* to a long day treatment in light of different spectral regions. From left to right: plants grown in red, green, blue and blue + infra-red light, 16 hrs per day, 900 μW/cm^2, 56 days after the beginning of the treatment.

Stolwijk *et al.* (1955) found that infra-red added to red light has a great effect on the flowering response of *Hyoscyamus niger.* In the following experiment infra-red was simultaneously added to red, green and blue light during 16 hrs per day. 3 or 4 different intensities of infra-red were used by treating the plants at different distances of the infra-red source.

In Table III the results are given of plants which were exposed during 4 weeks to this light treatment. At the end of the experiment the plants were kept another 5 weeks in long days in white light.

The intensity of the red and blue light was too high for flower initiation. Therefore an infra-red addition could not have any effect. Whereas this experiment was carried out simultaneously with the preceding one in which this intensity dependence was investigated, the long day effect of the red light intensity used in this experiment was still unknown. In green light a clear effect of the infra-red added was obtained and even the limit of activity was approached. Irradiated with 30 μW/cm^2 infra-red the main stem and the laterals situated at the side towards the infra-red source remained vegetative, whereas all laterals situated at the shadowside initiated flower primordia. Lower intensities of infra-red did not have any effect (Table III).

Table III

The influence of the addition of infra-red on the day length effect of a long day treatment in blue, green and red light on flower initiation of *Salvia occidentalis.* Duration of the treatment 28 days. Day temperature 22° C. Night temperature 17° C. Day length: 16 hrs of light per day.

Condition of the growing point						
16 hrs per day		Intensity of infra-red, added simultaneously (μW/cm^2)				
Spectral region	intensity μW/cm^2	0	25	30	40	60
blue	880	veg.	veg.	veg.	veg.	veg.
green	1200	gen.	gen.	veg.	veg.	veg.
red	3600	veg.	veg.	veg.	veg.	veg.

Representative plants of another experiment grown in green light with and without an addition of infra-red irradiation are shown in Fig. 4.

3. *Influence of light quality on the night break effect*

In a preleminary experiment it was found that red light is more effective than blue light in a night break treatment. The results of another experiment are presented in Table IV. The plants were exposed to a short day, 10 hrs of light per day, in white fluorescent light (1500 μW/cm^2). In the middle of the dark period groups of plants were exposed to blue or red light. The total amount of light was varied by using different exposure times, which did not exceed 10 minutes. It was also found that the effect of a dark interruption by red light can be reversed by an infra-red irradiation (Table IV).

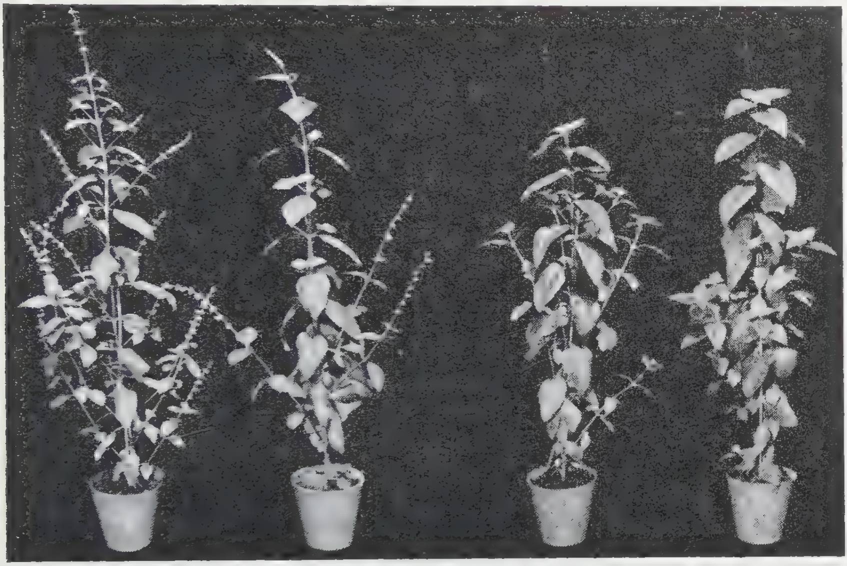

Fig. 4. The influence of an addition of infra-red on the day length effect of *Salvia occidentalis*, grown in 16 hrs green light per day. From left to right: plants grown in green light (900 μW/cm²) without infra-red (generative) and with 25 (generative), 40 (vegetative) or 60 μW/cm² infra-red (vegetative). 60 days after the beginning of the treatment.

Discussion

Until now it has been shown that only *Kalanchoe* (Wallrabe, 1943) and *Hyoscyamus niger* (Stolwijk *et al.*, 1955) have a special spectral requirement concerning the influence of the main light period on flowering.

The results presented in this paper make it obvious that *Salvia occidentalis*, a short day plant, has a similar spectral requirement as the long day plant *Hyoscyamus*.

In earlier experiments, Van der Veen could confirm Odén's statement, when growing lettuce in unfiltered neon and blue fluorescent light ("TL" 10). The difference was a quantitative one, the red light plants were flowering about two months earlier than the blue light plants.

Trifolium pratense showed the same reaction. This plant started bolting almost immediately when brought into a long day in neon light. Flowering occurred after 59 days. In blue light of the same intensity (1000 μW/cm²) plants were poorly flowering after 98 days.

From these experiments and from all the earlier work referred to in the introduction it is not possible to conclude whether there is

Table IV

Day lengthening effect of an interruption of the long dark period with red and blue light. Main light period 10 hrs white light per day (1500 μW/cm^2). Duration of the treatment 28 days. Day temperature 22° C. Night temperature 17° C. Observation 49 days after the beginning of the treatment. Number of plants 3.

Quantity of the light, interrupting the dark period. μW/cm^2 × sec.		Number of leaf pairs formed from the beginning of the treatment						% of laterals in vegetative condition
		generative plants			vegetative plants			
blue	27000	5	5	5				0
	54000	5	5	5				0
	108000	6	5	5				0
	216000	5	6	6				0
	432000	5	5	6				0
red	24000	7	6	7				0
	48000	6	9		> 9			50
	96000	5			> 10	> 10		50
	192000	7			> 9	> 8		60
red infra-red	384000 followed by 33600	5	5	5				0
control		5	5	4				0

an influence on flower initiation or only on the development of the flower primordia which might have been initiated in red light as well as in blue light. Moreover one cannot conclude which part of the spectrum has a special effect, because the light used was contaminated by light of other spectral regions. As was shown in the experiments described here a small contamination of infra-red, which is transmitted by the blue filter, may have a very strong elongating effect on plants, growing in blue light.

Also an addition of small amounts of infra-red light to 16 hrs of green light causes a long day effect on *Salvia*, which effect was not obtained in a long day in green light without this infra-red addition.

Whether Wallrabe (1943) working with *Kalanchoe* has used "pure" light or not is questionable as no characteristics of the filters in the infra-red region of the spectrum were given. At least the red light must have contained a contamination of infra-red radiation.

Stolwijk *et al.* (1955) concludes from Wallrabe's experiments that *Kalanchoë Blossfeldiana* has the same spectral requirement as *Hyoscyamus niger*, concerning the spectral activity of the photoperiod on flowering. Blue light was more promotive for flower initiation than red light, whereas green light did not induce flowering at all. However this conclusion is not correct.

In Wallrabe's *Kalanchoe* experiments a short day treatment was given, i.e. a daylength favourable for flower induction in this short day plant. In this case it was shown that a short day in red light is less effective in flower initiation than a short day in blue light;

whereas a short day in green light did not result in a short day effect. But the photoperiodic effect of a long day treatment in red, green and blue light on flowering has not been studied.

In the *Salvia* experiments however, a long day treatment was given, i.e. a daylength unfavourable for flower induction in this short day plant. For this plant it was shown that a long day in red is less effective in inhibiting flower initiation than a long day in blue light. Moreover a long day in green light did not have any long day effect at all, for flower formation was not inhibited.

This holds true for *Hyoscyamus niger* as well but, as this plant is a long day plant, flowering is initiated or is inhibited, when in *Salvia* flower initiation is inhibited, or is induced respectively.

Whether the "long day effect" of a long day treatment in red light of high intensity is due to the red light itself or to the unavoidable contamination of infra-red (in our experiments ± 2 % of the red radiation) is not sure.

However, it is not impossible that the action spectrum of the main light period will show some activity in the red part of the spectrum as well.

In the short day experiments an equal effect was obtained in red and in blue light.

The results of the night break experiments — red light being more effective than blue light — are in agreement with the action spectrum which has been thouroughly investigated by BORTHWICK and coworkers.

Examining a few other plant species (*Plantago major*, *Petunia hybr. Violacea*, *Arabidopsis thaliana*) we found clear indications that these plants too have the same spectral sensitivity for the main light period as *Salvia* and *Hyoscyamus*. It seems probable that this spectral requirement is a rather common phenomenon.

CONCLUSION

The results with *Salvia occidentalis* described above are in agreement with the response of *Hyoscyamus niger* described by STOLWIJK *et al.* (1955).

For *Hyoscyamus* and *Salvia* it is obvious that the photoperiodic effect is determined by at least two different photoreactions which have a completely different spectral sensitivity.

One of them, the reaction of the so called main light period, has the greatest activity in blue and infra-red.

In the other reaction, the so called night break, the red part of the spectrum is photoperiodically much more effective than light of the blue region. A red- infra-red antagonism exists in this night break reaction.

The statement of BONNER *et al.* (1953) that the main light period is only necessary for the production of photosynthates does not hold true for the plant species, mentioned above.

SUMMARY

1. *Salvia occidentalis* is an obligate short day plant.
2. However, flower initiation may occur after a long day treatment, depending on light intensity and the colour of the main light period.
3. In *Salvia occidentalis* as in *Hyoscyamus niger* the effect of a long day treatment is influenced by at least 2 different photoreactions.

ACKNOWLEDGEMENT

I am very much indebted to Dr. R. v. d. Veen for his interest and valuable remarks and to Miss J. C. Baars for her assistance.

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CONTRIBUTION À L'ÉTUDE DES TARAXACUM DE CORSE

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(*'s Gravenhage*)

(*reçu le 18 juin, 1957*)

INTRODUCTION

En 1952 M.le professeur R. de Litardière m'a envoyé une collection de *Taraxacum*, des plantes récoltées par lui et par ses colloborateurs en Corse et contenues dans son herbier. Cette collection importante, complétée pendant des années suivantes, est d'intérêt pour la connaissance de la flore de Corse comme pour celle de la taxonomie et la géographie du genre *Taraxacum*. Des espèces méditerranéennes y rencontrent, non seulement celles d'origine alpine, mais aussi des espèces habitant principalement l'Europe occidentale et boréale de climat modéré.

Je suis très vivement reconnaissant à M. de Litardière pour l'aimable secours et pour ses remarques critiques pendant mon étude.

1. SECT. OBOVATA v. S.

T. obovatum (Willd.) DC.

Cette espèce méditerranéenne occidentale, dont je n'avais vu jusqu'ici de spécimens provenant de Corse, a été découverte dans l'île près de Novella (17 V 1896) par FOUCAUD et SIMON (Trois Sem.herb. Corse 51, 149). Les échantillons récoltés par M. Simon et que M. de Litardière m'a communiqués sont défleuris et privés d'akènes; je ne puis donc savoir si les plantes appartiennent à la sous-espèce typique à akènes rougeâtres (*Leontodon obovatus* Willd.) ou bien à la sous-espèce *ochrocarpum* v. S. à akènes jaunâtres. M. de Litardière a retrouvé le T. *obovatum* dans une localité de la Corse orientale: entre Piano et le col de St. Antoine, au bord de la route, pelouses a 700 m., 9 V 1951; la sous-espèce typique est récoltée par C. PELGRIMS: vallée de la Restonica, 1 VI 1957.

2. SECT. ERYTHROSPERMA Dt. em. Lindb.f.

T. atrosquamatum v. Soest **nov. sp.** (Fig. 1).

Planta gracilis ca 15—20 cm alta subglabra.

Folia erecta luteo-viridia (nervo mediano pallido) petiolis angustissimis rubro-violaceis. Folia exteriora oblanceolata denticulata vel dentata vel incisa; folia interiora utrinque ca 4 loba; lobi laterales inferiores angusti subfiliformes (interlobiis angustis), superiores triangulares interdum retroversi dorso subdentati margine inferiore saepe

integro recto vel concavo (interlobiis latiusculis); lobus terminalis magnus hastatus sublongus saepe subobtusus inferne grosse dentatus.

Scapi subnumerosi tenues foliis breviter superantes subglabri.

Involucrum mediocre basi rotundatum obscure viride; squamae exteriores adpressae ovatae ca 4.5 mm longae ca 2.5 mm latae ciliolatae conspicue albo- vel purpureo-marginatae apice purpureae p.p. minute corniculatae; squamae interiores late lineares apice callosae.

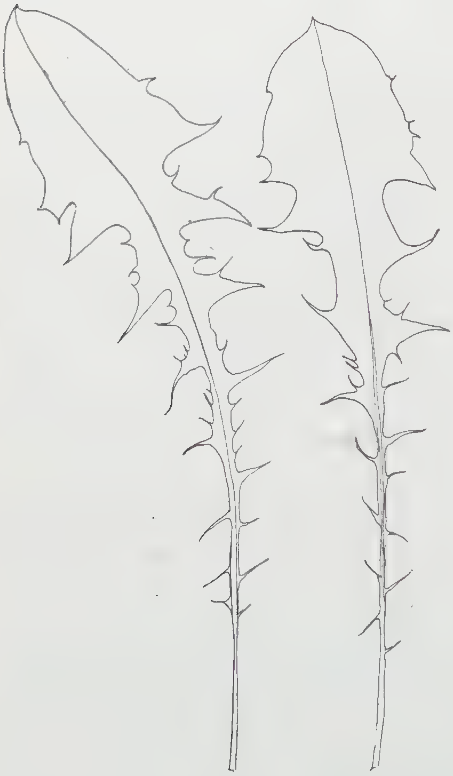

Fig. 1. *T. atrosquamatum* v. S.; ½ ×

Calathium saturate luteum; ligulae marginales planae extus stria cano-violacea notatae; antherae polliniferae, stylus et stigmata obscuri. Floret vere.

Achenium fulvum 5 mm longum (pyramide inclusa) superne grosse spinulosum ceterum rugosum, basi laeve, in pyramiden cylindricam 1.0 mm longam abrupte abiens; rostrum 8 mm longum, pappus albus 6 mm longus.

E sectione Erythrospermorum.

Santa-Maria-di-Lota, près du pont sur la rivière de Miomo, route de Pietranera, T. Marchioni, 4 V 1955.

T. braun-blanquettii v. S.

Des plantes, en tout cas très proches de cette espèce de l'Europe sud-ouest, ont été récoltées entre Canale-di-Verde et Linguizetta, fossé herbeux frais de la route, T. Marchioni, 10 IV 1954.

T. castaneum v. Soest **nov. sp.** (Fig. 2).

Planta gracilis ca 25 cm alta.

Folia erecta laete gramineo-viridia parce araneosa petiolis sordide purpureis. Folia interiora 15—25 cm longa (petiolo inclusa) multilobata; lobi laterales patentes vel erecto-patentes lanceolati vel lineares 1—3 mm lati dorso interdum dentati margine inferiore interdum 1 dente longo muniti, interlobiis ca 2—3 mm latis saepe longe patento-dentatis dentibus similibus lobis; lobus terminalis ± sagittatus dentatus vel denticulatus vel integer, lobulis basis similibus lobis lateralibus, lobulo apicis ca 3 mm lato ad 15 mm longo subobtuso; folia exteriora similes minus lobata et dentata.

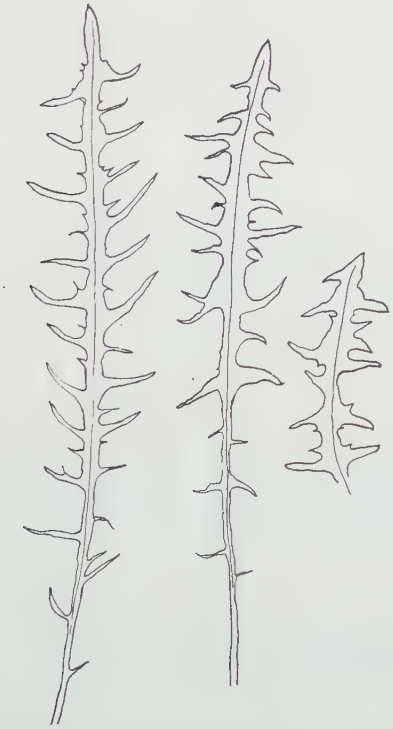

Fig. 2. *T. castaneum* v. S.; ½ ×

Scapi paulo araneosi.

Involucrum gracile 12 mm longum 9 mm latum viride. Squamae exteriores apice recurvato ovato-lanceolatae acuminatae 7 mm longae ad 2.5 mm latae late albo- vel purpureo-marginatae (margo ad 0.3 mm latus) purpurascentes laeves; squamae interiores late lineares membranaceo-marginatae sub apice callosae.

Calathium paulo radians (?); ligulae 15 mm longae clare luteae, marginales planae extus stria atro-violacea notatae; antherae vacuae, stylus et stigmata lutei. Floret vere.

Achenium castaneum 4.0 mm longum (pyramide inclusa) superne spinulosum ceterum rugosum in pyramiden cylindricam ca 1 mm longam (spinulis saepe praeditam) subabrupte abiens. Rostrum 10 mm longum, pappus albus 6 mm longus.

E sectione Erythrospermorum.

Vescovato, bords de la route de Venzolasca, après le pont de Piova, T. Marchioni, 21 IV 1954.

T. fulviforme Dt.

Cette espèce méditerraneo-atlantique est commun en Corse: Murato, rives du Bevinco, R. de Litardière, 8 IV 1936; Vescovato, châtaignerie du Gaglinu di i Frati, à droite de la route de Venzolasca, 220 m, R. de Litardière, 20 V 1953; sables de la Casaluna, près du pont de la route de S. Lorenzo à Francardo, 240 m, R. de Litardière, 4 IV 1928; au dessus de Lavatojo, S. de Corte, pineraie, 700 m, R. de Litardière, 24 V 1935; Vizzavona, la Foce, bords de la route, C. Pelgrims, 26 V 1952.

f. achyrocarpum v. Soest nov. f.: achenia roseolo-ochracea:

Olmo, route de Monte, châtaigneraie, 550 m, R. de Litardière, 19 V 1953; entre Milaria et Pied' d'Alesani, talus rocheux au tournant de Pinzuti, 725 m, R. de Litardière, 27 V 1953; entre Felce et Milaria, 765 m, R. de Litardière, 19 V 1953.

T. fulvum Raunk.

Des plantes affines à cette espèce ont été trouvées à Chisoni, R. Rotgès, 23 III 1898.

T. gasparrinii Tin. ex Lojac.

Cette espèce méditerranéenne occidentale est récoltée en Corse: Mte Felce, S. de Corte, pelouses sur granite, R. de Litardière, 24 V 1935.

T. lacistophyllum (Dt.) Dt.

Cette espèce de l'Europe occidentale est trouvée en Corse:

Olmo, route de Monte, châtaigneraie, 550 m en compagnie de *T. fulviforme* et *T. rubicundum*, R. de Litardière, 19 V 1953.

T. purpureo-cornutum v. Soest **nov. sp.** (Fig. 3).

Planta humilis gracilis ca 12 cm alta, basi fragmentis foliorum vetustorum paulo incrassata, inferne glabrescens.

Folia 5 cm longa decumbentia gramineo-viridia glabra nervo mediano pallido vel parum colorato, petiolis brevibus violaceis. Folia exteriora oblanceolata lobata, lobi laterales triangulares retroversi dorso breviter dentati, lobus terminalis sagittato-hastatus obtusiusculus parce dentatus. Folia interiora (utrinque 4-5)-lobata, lobi laterales angusti retroversi vel p.p. patentes vel erecto-patentes mar-

gine inferiore et dorso saepe dentibus brevibus vel sublongis praediti, interlobiis latiusculis dentatis; lobus terminalis breviter triangulariter hastatus.

Scapi ca 3 purpureo-violacei foliis valde superantes sub involucro araneosi.

Involucrum mediocre 12 mm longum laete viride. Squamae exteriores apice recurvato lanceolatae 4.5 mm longae 1 mm latae purpurascentes inconspicue marginatae callosae vel corniculatae, interiores late lineares membranaceo-marginatae sub apice colorato purpureo-cornutae vel -corniculatae.

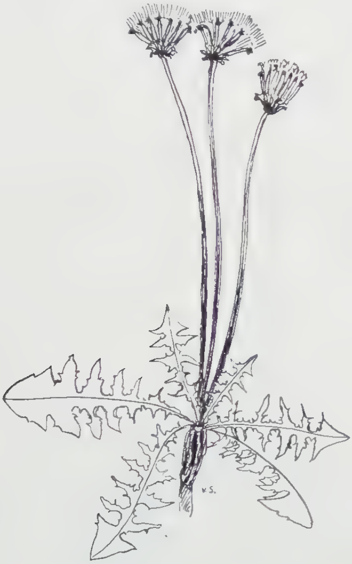

Fig. 3. *T. purpureo-cornutum* v. S.; ½ ×

Calathium clare luteum. Ligulae marginales extus stria cano-violacea notatae; antherae polline carentes; stylus et stigmata obscuri subnigri. Floret vere.

Achenium badio-rubrum 4 mm longum (pyramide inclusa) superne spinulosum ceterum tuberculatum, in pyramiden cylindricam 1 mm longam abrupte abiens; rostrum 8 mm longum; pappus albus 6.5 mm longus.

E sectione Erythrospermorum.

Entre Piano et le col de St.Antoine, bord de la route, pelouses et ptéridaie, R. de Litardière, 29 V 1951, en compagnie de *T. fulviforme* et *T. roseocarpum*.

T. roseocarpum v. Soest **nov. sp.** (Fig. 4).

Planta gracilis parce araneoso-pilosa 6—18 cm alta basi fragmentis foliorum vetustorum subincrassata.

Folia ad 12 cm longa gramineo-viridia petiolis brevibus nervoque mediano praesertim parte inferiore rubro-violaceis, interiora multilobata; lobi laterales angusti lanceolati vel subfalcati (summo erecto vel ± retroverso) acuti integres vel raro denta una praedita vel ± denticulati, interlobiis angustis dentis longis (ad 5 mm) praeditis; lobus terminalis parvus deltoideus, lobulo apicali integro saepe ± contracto subacuto.

Scapi tenues 2 vel numerosi foliis superantes purpurei sub involucro araneosi.

Involucrum mediocre 9 mm longum 12 mm latum viride. Squamae exteriores reflexo-patentes lanceolatae 5 mm longae 1.7 mm latae conspicue marginatae corniculatae apice pallide roseolo, interiores lineares membranceo-marginatae corniculatae.

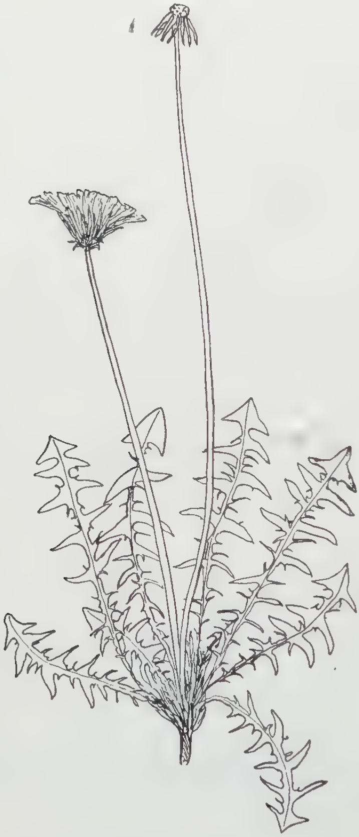

Fig. 4. *T. roseocarpum* v. S.; ½ ×

Calathium planum radians ad 2.5 cm diametro ± pallide luteum. Ligulae marginales extus stria rubro-violacea notatae. Antherae vacuae; stylus et stigmata sordide lutei. Floret vere.

Achenium roseo-fulvum vel fulvescens parvum 3 mm longum (pyramide inclusa) ad 0.7 mm latum superne spinulosum ceterum ± laeve, in pyramiden subcylindricam ± 0.7 mm longam laevam subsensim abiens; rostrum 8 mm longum, pappus niveus 5 mm longus.

E sectione Erythrospermorum.

Entre Loreto-di-Casinca et le col de St.Augustin, près du lieu dit Pozzo, châtaigneraie sèche, 700 m., R. DE LITARDIÈRE, 31 V 1951. Puis: entre Piano et le col de St.Antoine, bord de la route, pelouses et ptéridaie, 700 m, R. DE LITARDIÈRE, 29 V 1951.

Cette espèce est affine aux *Taraxacum* à akènes fauves et aussi au *T. gasparrinii*, dont elle diffère par les folioles involucrales plus étroites et moins corniculées et recourbées et par la forme des feuilles moins divisées. Elle ressemble au *T. purpureo-cornutum*, mais n'en a pas les grandes cornes ni les akènes rouges.

T. rubicundum (Dt.) Dt.

Cette espèce de la moitié occidentale de l'Europe atteigne la région méditerranéenne de France et est aussi récoltée en Corse:

Mte Secco, près du col du Teghime, fentes des rochers de cipolin près du sommet, R. DE LITARDIÈRE, 9 IV 1936; puis: Olmo, route de Monte, châtaigneraie, 550 m, R. DE LITARDIÈRE, 19 V 1953.

T. silesiacum Dt. ex Hagl.

Cette espèce de l'Europe centrale, atteignant l'Europe occidentale et boréale à climat modéré, est récoltée aussi en Corse:

Col de Vergio, J. BONFILS, 23 V 1950.

T. squamulosum v. Soest **nov. sp.** (Fig. 5).

Planta gracilis 12—20 cm alta parce araneoso-pilosa.

Folia laete gramineo-viridia nervo mediano pallido, petiolis ± purpureis angustissimis; folia exteriora lobata (utrinque 3 loba), lobi laterales triangulares dorso ± dentati, interlobiis latis subdentatis-lobus terminalis sat magnus triangularis vel plerumque hastatus ob, tusus ± dentatus saepe inciso-dentatus. Folia interiora (utrinque

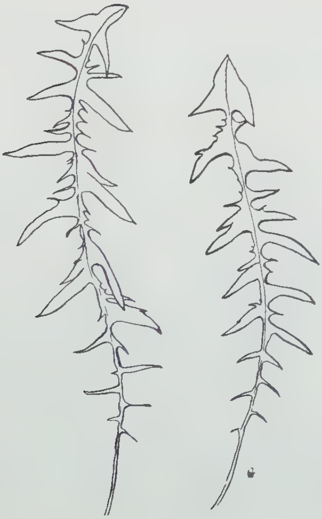

Fig. 5. *T. squamulosum* v. S.; ½ ×

4—5 loba) ad 16 cm longa (petiolis inclusa) 2—3 cm lata, lobi laterales angusti lineares, lanceolati vel falcati, integres vel dorso et raro margine inferiore saepe 1 dente longo muniti, vel incisi, interlobiis ± longis angustis valde dentatis; lobus terminalis vulgo ± sagittatus vel hastatus (summo obtuso) integer, lobulo apicali saepe valde contracto obtuso vel acuto, lobulis basalibus saepe elongatis.

Scapi foliis breviter superantes.

Involucrum mediocre 12 mm longum 9 mm latum obscure viride. Squamae exteriores ± adpressae apice recurvato ovatae ca 5 mm longae ca 3 mm latae late albido-marginatae ciliatae p. max. p. callosae, interiores late lineares ± callosae.

Calathium subradians pallide luteum; ligulae marginales extus stria obscure cano-violacea ornatae; antherae polliniferae; stylus et stigmata fusco-virescentes. Floret vere.

Achenium fulvum 4.0 mm longum (pyramide inclusa) 1.2 mm latum superne late subbreviter spinulosum ceterum valde rugosum in pyramiden laevam breviter cylindricam (0.4 mm longam) abrupte abiens. Rostrum 8 mm longum, pappus albus 6 mm longus.

E sectione Erythrospermorum.

Pietralba, au S.-W. de la gare, bord d'un ruisseau, R. DE LITARDIÈRE, 4 IV 1936; puis: Barchetta, rive gauche de la Casacconi, 120 m, R. DE LITARDIÈRE, 2 IV 1928.

Cette espèce est affine au *T. braun-blanquettii*; les akènes sont fauves et non d'un rouge-orangé; les épines sont assez larges et courtes, non fines et minces; les akènes ont leur plus grande largeur vers le sommet et non dans la partie médiane. Les folioles involucrales sont munies partiellement de petites callosités et ne sont pas corniculées, les folioles extérieures sont plus courtes et plus ou moins pressées contre l'involucre.

T. tortilobum Florstr.

Cette espèce de l'Europe occidentale, seulement introduite dans l'Europe boréale, a été trouvée en Corse:

Olmo, route de Monte, fentes de rochers schisteux, 560 m, R. DE LITARDIÈRE, 19 V 1953; Vizzavona, la Foce, bords de la route, C. PELGRIMS, 26 V 1952.

3. SECT. VULGARIA Dt.

T. marchionii v. Soest **nov. sp.** (Fig. 6).

Planta ca 20 cm alta sublonge araneoso-pilosa.

Folia gramineo-viridia 20 cm longa (petiolo subangusto ± purpureo-colorato inclusa) utrinque 5 loba; lobi laterales triangulares in foliis interiores fissi vel incisi vel forte et longe dentati dentibus patentibus, summo lineares lingua-lati (pars linearis 1—1.5 cm longa); interlobiis angustis elongatis dentatis vel denticulatis; lobus terminalis ± deltoideus vel in foliis interiores saepe trilobatus, lobulis basis angustis late linearis subobtusis, lobulo apicis primo inserrato secundo latiore tertio lanceolato-elongato, summo subobtuso.

Scapi sub involucro dense longe araneosi.

Involucrum viride 13 mm longum 15 mm latum; squamae exteriores reflexo-patentes lanceolatae ca 8—9 mm longae ca 3 mm latae anguste marginatae; squamae interiores late lineares membranaceo-marginatae.

Calathium planum radians ad 3 cm diametro. Ligulae luteae, marginales planae extus stria fusco-violacea notatae; antherae polliniferae, stylus et stigmata sordide lutei. Floret vere.

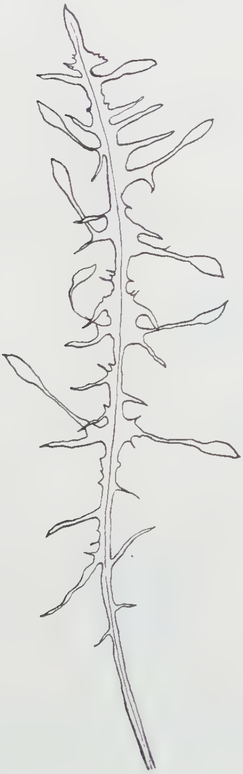

Fig. 6. *T. marchionii* v. S.; ½ ×

Achenium parvum 3.5 mm longum (pyramide exclusa) pallide brunneum superne spinulis patentibus munitum ceterum rugosum — basi laeve, in pyramiden conicam 0.4 mm longam (spinulis saepe praeditam) subsensim abiens; rostrum breve 6—7 mm longum, pappus albus 6 mm longus.

E sectione Vulgariorum.

Bords de la route de Vescovato à Venzolasca, avant le cimetière, T. Marchioni, 14 IV 1954.

Les *Vulgaria* ne sont pas communs dans la région méditerranéenne; aussi en Corse, ne sont-ils pas nombreux; outre *T. marchionii*, j'ai vu plantes de cinq localités, tous non bien identificables.

4. Sect. Pachera v. S.

T. litardieri v. Soest **nov. sp.** (Fig. 7).

Planta humilis gracilis ca 4—7 cm alta inferne araneoso-pilosa. Folia decumbentia vel subdecumbentia laete gramineo-viridia vel sublutescentia glabra petiolis subalatis pallidis. Folia exteriora oblanceolata integra vel sublobata, interiora (utrinque ca 3—) lobata; lobi laterales integres deltoidei vel triangulares — hastati, apici p.max.p. retroflexi, interlobiis latiusculis; lobus terminalis brevibus, triangularis vel subhastatus obtusus — subobtusus vel p.p. inconspicue acuminatus.

Scapi foliis aequilongi paulo (sub involucro conspicue) araneosi. Involucrum parvum obscure viride; squamae exteriores ± erecto-patentes ovatae—lanceolatae, 3—4 mm longae ad 2 mm latae, subacuminatae inconspicue vel im-marginatae; squamae interiores lineares ca 10 mm longae.

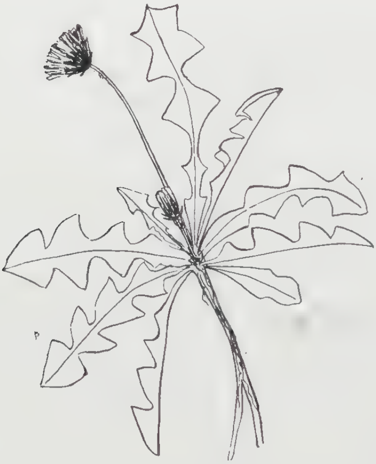

Fig. 7. *T. litardieri* v. S.; ½ ×

Calathium subclausum ad 1.2—1.5 cm diametro luteum; ligulae tubulosae marginales subnigrae; antherae vacuae, stylus et stigmata fusco-virescentes. Floret aestate.

Achenium stramineum parvum 3.5 mm longum (pyramide inclusa) superne minute spinulosum ceterum glabrum, in pyramiden conicam ca 0.5 mm longam inconspicue abiens. Rostrum breve, 2.5—3 mm longum; pappus sordide albus 4—5 mm longus.

E sectione Pacherorum.

Punta Artica, éboulis morainiques, 2250 m, R. de Litardière, 2 VIII 1908. Puis: Monte Rotondo, versant du lac de Pozzolo, rocailles, 2500 m, R. de Litardière, 25 VIII 1919; ibid., éboulis au dessus du lac d'Oriente, 2200 m, R. de Litardière, 13 VIII 1908; Massif du Rotondo, au dessous du lac Cavaccioli, pelouses à *Sagina pilifera,* 1890 m, R. de Litardière, 1 VIII 1932.

Ensuite, dans les Alpes Maritimes: éboulis entre le lac de Rabuons et le lac supérieur, 2650 m, R. DE LITARDIÈRE, 7 IX 1919.

Les plantes de Punta Artica et du Monte Rotondo ont été déterminées par ROUY comme *T. alpestre* (DC.) var *Pacheri* (Schultz-Bip.) Rouy. En tout cas l'espèce est affine au *T. pacheri* Schultz-Bip., dont cependant les fleurs sont oranges et moins fermées, dont les ligules sont planes et non tubuleuses et dont les akènes diffèrent aussi un peu.

5. SECTION . . .

T. cucullatiforme v. Soest **nov. sp.** (Fig. 8).

Planta humilis ca 6—10 cm alta.

Folia decumbentia sublutescentia glabra ca 5 cm longa petiolis alatis brevissimis pallidis. Folia obovata obtusa integra vel paulo recurvato-lobata.

Scapi foliis paulo superantes ± araneoso-pilosi.

Involucrum mediocre obscure viride; squamae exteriores erecto-patentes lanceolatae 6 mm longae 2.2 mm latae ciliolatae apice subviolaceo, interiores lineares 13 mm longae.

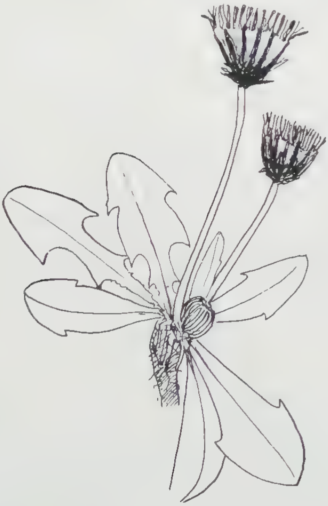

Fig. 8. *T. cucullatiforme* v. S.; ½ ×

Calathium subclausum; ligulae flavae omnibus involutae, marginales stria obscure violacea notatae summo subnigrae; antherae polliniferae, stylus et stigmata nigri. Floret aestate. Achenium ignotum (pappus albus).

Corse: Massif du Renoso, Punta di Oriente, pelouses entre les rochers au dessous du sommet, 2000 m, E. MALCUIT, 11 VII 1938 et 5 VII 1941.

Cette espèce diffère du *T. cucullatum* Dt. et de quelques autres formes par les fleurs d'un jaune moins pâle, par les stries obscures, la forme des folioles extérieures de l'involucre, la tige plus ou moins poilue, etc.

6. Section . . . .

T. renosense v. Soest **nov. sp.** (Fig. 9).

Planta mediocris ca 15—20 cm alta basi fragmentis foliorum vetustorum paulo incrassata, glabrescens.

Folia numerosa ca 10 longa (petiolis subangustis pallidis inclusa) suberecta sublutescentia subglabra. Folia interiora lobata (utrinque 3 loba), lobi laterales subtriangulares subobtusi dorso interdum dentati, margine inferiore saepe concavi integri, interlobiis interdum 1-dento grosso muniti; lobi inferiori saepe perbreves vel folia in petiolo parte superiore late alato magis dentato contracta; lobus terminalis sat magnus hastatus subobtusus interdum breviter denticulatus vel ovato-trangularis vel ovato-sagittatus, raro profunde incisus, lobulo apicali triangulares vel ovati. Folia exteriora angustiora minus lobata.

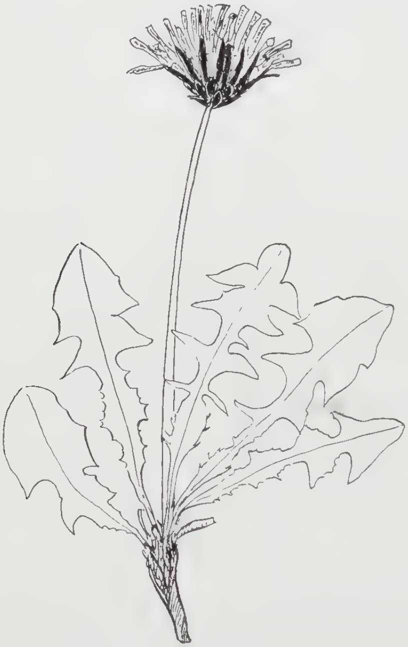

Fig. 9. *T. renosense* v. S.; ½ ×

Scapi pallidi foliis superantes sub involucro araneosi.

Involucrum subcrassiusculum basi rotundatum viride. Squamae exteriores laxe adpressae ovatae ca 6 mm longae ca 3 mm latae acuminatae late (0.3 mm) marginatae ecorniculatae; squamae interiores late lineares inferne membranaceo-marginatae ca 14 mm longae.

Calathium planum radians ad 35 mm diametro saturate luteum. Ligulae marginales planae extus stria purpurea ornatae; antherae vacuae, stylus et stigmata fusco-virescentes. Floret aestate.

Achenium 4 mm longum (pyramide inclusa) ochraceum superne

breviter late spinulosum ceterum rugosum — basi laeve, in pyramiden conicam laevam 0.35 mm longam subsensim abiens; rostrum 8 mm longum, pappus albus 6—7 mm longus.

Monte Renoso, rochers du sommet, 2357 m, R. de Litardière, 16 VII 1907; puis: Monte Rotondo, rochers de la Calanca di Rinoso, 2600 m, R. de Litardière, 13 VIII 1908.

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CELL-WALL STRUCTURE OF SOME MONOCOTYLEDONES

B. VAN DER HOUVEN VAN OORDT-HULSHOF
(*'s Gravenhage*)

(*received May 13th*, 1957)

1. Introduction

Numerous studies have been reported about the swelling of cellulose walls of fibres and hair and the accompanying phenomena. A historical survey of these investigations was published by Mangenots and Raison (1951).

When the "Querhaut-Theorie" of Lüdtke (1928) had been refuted, it was generally held that the formation of bead-strings in swelling fibres and hair is caused by a swelling anisotropy of two successive layers in the cell wall. It was thought that a layer which swells strongly in transverse direction (to the cell axis) is surrounded by a layer swelling less, or not at all, in that direction. Further it was supposed that a bead is formed if, because of a fissure in the outer layer, the strongly swelling inner layer pours out through this fissure.

The difference in swelling of two layers of a cell wall can be caused by a different chemical composition as well as, in the case of a cellulose wall, by a difference in orientation direction of the cellulose chains. A cellulose wall (or wall layer) whose main direction of orientation is approximately parallel to the axial direction of the cell will swell strongly in transverse direction; a wall (or wall layer) in which the chains are mainly oriented transversely to the cell axis will not swell in transverse direction or only very little so.

The non-swelling or little-swelling outer layer of fibres and hair can be:

a) the primary wall in which a transverse orientation predominates (Frey-Wyssling, 1941; Roelofsen, 1951; a.o.);
b) the outer part of the secondary wall (Bailey and Kerr, 1935);
c) an outer layer of different chemical composition;
d) a combination of two or more of these components.

With regard to the swelling of some monocotyledones, e.g. *Andropogon sorghum*, *Arundo donax*, *Pandanus*, and some species of bamboo, it has been observed that inside a bead-string a second bead-string can form, and again inside the latter sometimes a third. From this it follows that the wall of these fibres consists of several concentric layers, each corresponding with the wall of a "normal" fibre (Lüdtke, 1928 and 1935; Anna Schlottmann, 1933; Bailey and Kerr, 1935; Griffioen, 1935; Sachet, 1946; Mangenots and Raison, 1951).

Various investigators observed that in the swollen fibre the above-mentioned composed concentric layers in many places are lying loose and can slide along each other.

ANNA SCHLOTTMANN (1933) incidentally mentioned how on swelling of bamboo fibres the "tubes" which together form the cell wall telescoped out ("teleskopisch auseinander schoben").

Several workers observed that in a broken fibre the various layers at the surface of the fracture dissolve in the swelling medium (particularly in cuprammonium) with different speed, the cell assuming the form of a pulled-out telescope.

2. MATERIAL

The swelling phenomena of this study have been observed on pulps of some monocotyledones, particularly on those of sugar cane.

Pulp of a fibre-producing plant is a macerated, more or less delignified mass of the fibre-producing tissue of the plant, usually of the stalk or stem. In monocotyledones fibres mainly originate from the sclerenchyma sheath of vascular bundles.

Pulp is generally made by heating with NaOH, an alkaline sulphide, or a sulphite solution. After this process, the cell walls often still contain lignin which can be eliminated by a bleaching process. For this purpose chlorine is used in the form of chlorine gas, chloride of lime, or hypochlorite.

Cross-sections were made from alcoholic specimens of sugar cane and *Andropogon sorghum*, and the dry stalk parts of various kinds of bamboo.

As a swelling medium cuprammonium was used. Some comparing observations have been made with other swelling media which are mentioned below.

3. LIGHT MICROSCOPE STUDIES ON PULPS

a. Pulp of sugar cane, with cuprammonium as a swelling medium

On swelling bleached, lignin-free, pulp of sugar cane in cuprammonium, diluted with three to four parts of concentrated ammonia solution, it is seen that in the cell walls of many fibres there are layers that begin to separate. These layers loosen in many places and lie in curves and twists inside each other (Fig. 1). The fracture surface of a broken fibre soon changes into the well-known image of the pulled-out telescope (Fig. 2), as has been described for other monocotyledones.

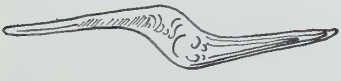

Fig. 1. Swollen fibre of the short type

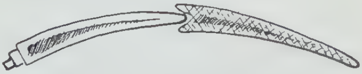

Fig. 2. The "inner tip" of a fibre has escaped from the "outer tip"; the fracture surface shows the form of a pulled-out telescope

If some drops of cuprammonium are drawn through a cover-slipped pulp specimen in water or ammonia solution, swelling proceeds less gradually, and the following phenomena are observed:

1. In a broken-off fibre tip the various concentric "tubes" which form the cell wall telescope out, some slowly, others quickly, so that after some time two or more fibre tips come to lie in line and level with each other (Fig. 2, 3 and 4). It appears as if the inner tubes are pushed with force out of the surrounding tube. This impression is even more striking in the following phenomenon:

2. If a bead has been formed in a fibre rather close to the tip, an "inner tip" can be pushed by the surrounding "outer tip" in the direction of the bead. In the bead this inner tube is pressed into curves until the tip of the inner tube has entered the bead. At that moment the inner tube breaks through the swelling cellulose which forms the wall of the bead, and stretches itself with a swing out of the fibre, so that this fibre has got two ends. Fig. 5 shows a fibre which, in that way, has got a double tip at both ends.

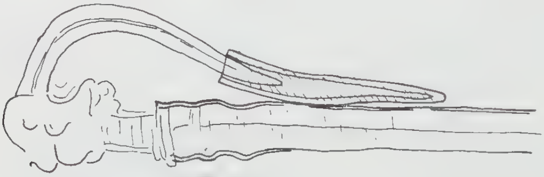

Fig. 4. The same stage as in Fig. 2

3. Not only in fibres but also in sclereids and parenchyma cells "inner and outer cells" telescope out. In these more or less isodiametric elements no beads are formed, but from time to time a whole wall collapses, and then two to four cell-wall layers can telescope out as intact cell surroundings, slowly or quickly, at the same time or one by one. Lüdtke (1928), although not giving an exact description, reported on a phenomenon in bamboo which may be identical herewith.

In sugar cane no sharp limits can be drawn between parenchyma cells, sclereids and fibres, but all intermediate forms are found. It is therefore not surprising that these cell types which are often said to bear little resemblance as to the structure of their cellulose wall, behave in an analogical way in this respect.

In bleached pulp of sugar cane, also if made by a process different from that described above, these phenomena are frequently seen. In exceptional cases they can also be observed in unbleached pulp.

On swelling in cuprammonium some fibres, almost all parenchyma cells, and few sclereids show a distinct fibrillisation striation. Each cell-wall layer, telescoped off or out, shows a similar striation. Almost without exception this striation has a Z-spiral orientation.

b. Pulp of other monocotyledones, with cuprammonium as a swelling medium

The phenomena described above can also be observed on pulp of *Bambusa arundinacea*, species of *Melocanna*, and *Andropogon sorghum* (*saccharatum*).

We did not succeed in obtaining these phenomena on pulp of cereal straw (probably *Triticum sativum*), *Oryza sativa*, *Pandanus* spec.

c. Pulp of sugar cane, with other swelling media

For obvious reasons, the swelling proceeds much more slowly in saturated $ZnCl_2$ solution, phosphoric acid 75 %, and NaOH 20 % than in cuprammonium. There is usually no bead formation. The telescoping-out also occurs infrequently, though the layers of the cell wall show a distinct loosening from each other. Only a few times a telescoping-out phenomenon has been observed in saturated $ZnCl_2$ solution and in phosphoric acid solution, both spontaneously or after exerting pressure on the cover-slip.

4. POLARIZATION MICROSCOPE STUDIES ON PULPS

In polarized light between crossed nicols all fibres show a positive birefringence (to the longitudinal axis of the cell). Parenchyma cells and sclereids have a positive or negative double refraction, or are isotropic. One half of a sclereid or parenchyma cell may show a positive, the other half a negative birefringence.

In the orthogonal position of the fibres there is no extinction. Is a compensator plate, red 1st order, inserted between preparation and analyzer, then the fibres show addition colours in the orthogonal position parallel to the vibration plane of the polarizer; this is an indication of a Z-spiral orientation of the cellulose micelles (NAEGELI and SCHWENDENER, 1877; FREY-WYSSLING, 1941).

Not only the intact wall but also walls missing one or more layers which have been telescoped off or out, always show the colour indicating a Z-spiral orientation. It was too difficult to determine the colour in the separate telescoped layers, probably because the part of the layer that is not yet swollen and is, therefore, still birefringent, is very thin.

5. STUDIES ON CROSS-SECTIONS

Cross-sections through the stalk of sugar cane, bamboo, and *Sorghum* show that the wall of the fibres is layered. This layered structure is clearly seen in the wall that is swollen in H_2SO_4 solution 62% (Fig. 6). Also in the wall of non-treated parenchyma cells high magnification reveals a layered structure (Fig. 7).

In polarized light between crossed nicols, the cell walls of sugar cane (Fig. 8) and *Sorghum* show dark and light concentric rings in the cross-sections of sclerenchymatic cells and parenchyma cells. BAILEY and KERR (1935) described the same observation for the fibres of *Pandanus*, PRESTON and SINGH (1951) for bamboo.

6. Electron microscope studies

For the study of cell walls with the electron microscope replicas from the cross-sections of sugar-cane stalk were made. From Fig. 9 it is clearly seen that the secondary wall of a fibre consists of at least three layers.

Fig. 10 illustrates the high degree of fibrillisation in the layer adjoining the lumen of the cell. The replica film that covered that wall layer is folded back here, and lies in the plane of the micrograph. The direction of fibrillization here too indicates a Z-spiral orientation.

The almost round pits in a strongly oriented wall, or at least in the wall layer may be incidentally mentioned.

An attempt to determine the absolute direction of orientation in the various layers by making oblique sections met with too many technical difficulties.

7. Discussion

From the observations described above it appears that the cell wall of the examined fibres, sclereids and parenchyma cells is built up of several layers. In a swollen condition of the bleached pulp these layers lie loose, and can easily slide along each other. Upon the periphery of these layers, except upon that of the outer one, a pressure is exerted then in the direction of the lumen. By this radial pressure the layers are squeezed out as soon as an opening occurs somewhere in the outer layer of the cell wall (formation of a bead). The radial pressure upon the whole periphery of a certain layer is exerted by the surrounding layer. Each layer swells towards the lumen. Because the outside of a layer does not swell, it does not distend, and thus the whole swelling pressure of the inner part is directed towards the lumen. During swelling and dissolving in cuprammonium the peripheral part of a layer maintains the form of the cell longest. Usually, the inner part of the layer soon becomes a formless mass — unless it is prevented from distending —, for instance, if a single layer has slipped off of a cell wall and lies free in the swelling medium. In a cell from which an inner layer of the cell wall is slipping out, it can be seen that immediately behind that layer the lumen is filled with swelling cellulose from the surrounding layer (Fig. 3).

Loose layers slipped-out of fibre tips often form beads immediately after their release.

On account of the picture of the cross-sections between crossed nicols, it may be concluded that the different properties of the two concentric parts of a cell-wall layer are due to a difference in orientation direction of the cellulose chains. The angle formed by the main orientation direction and the cell axis is greater in the outer part of the layer than in the inner part. The outer part produces the bright rings in the cross-section, the inner part the dark ones.

Preston and Singh (1950, 1952) using another method, reported the same cell-wall structure for the fibres of *Bambusa arundinacea*, *Melocanna bambusoides* and some species of the genus of *Dendrocalamus*.

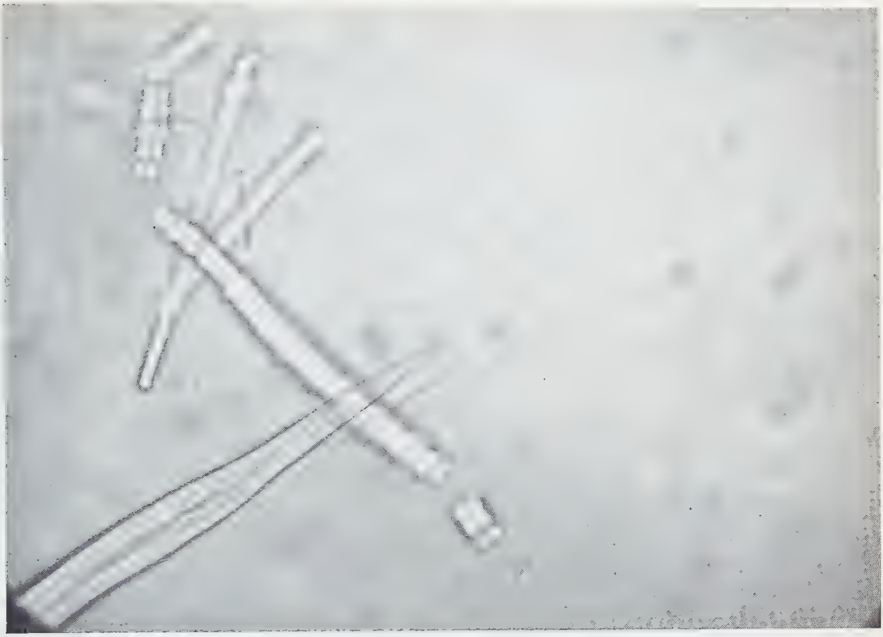

Fig. 3. The same stage as in Fig. 2; the fibre lies across another swelling, telescope-ended one

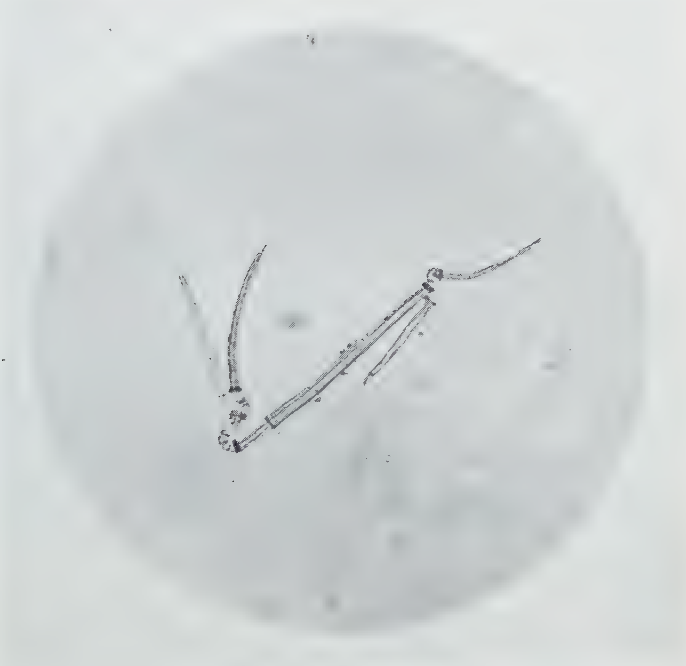

Fig. 5. Two beads have been formed in one fibre; two "inner tips" have slipped out of two "outer tips", that are still in connection with the fibre

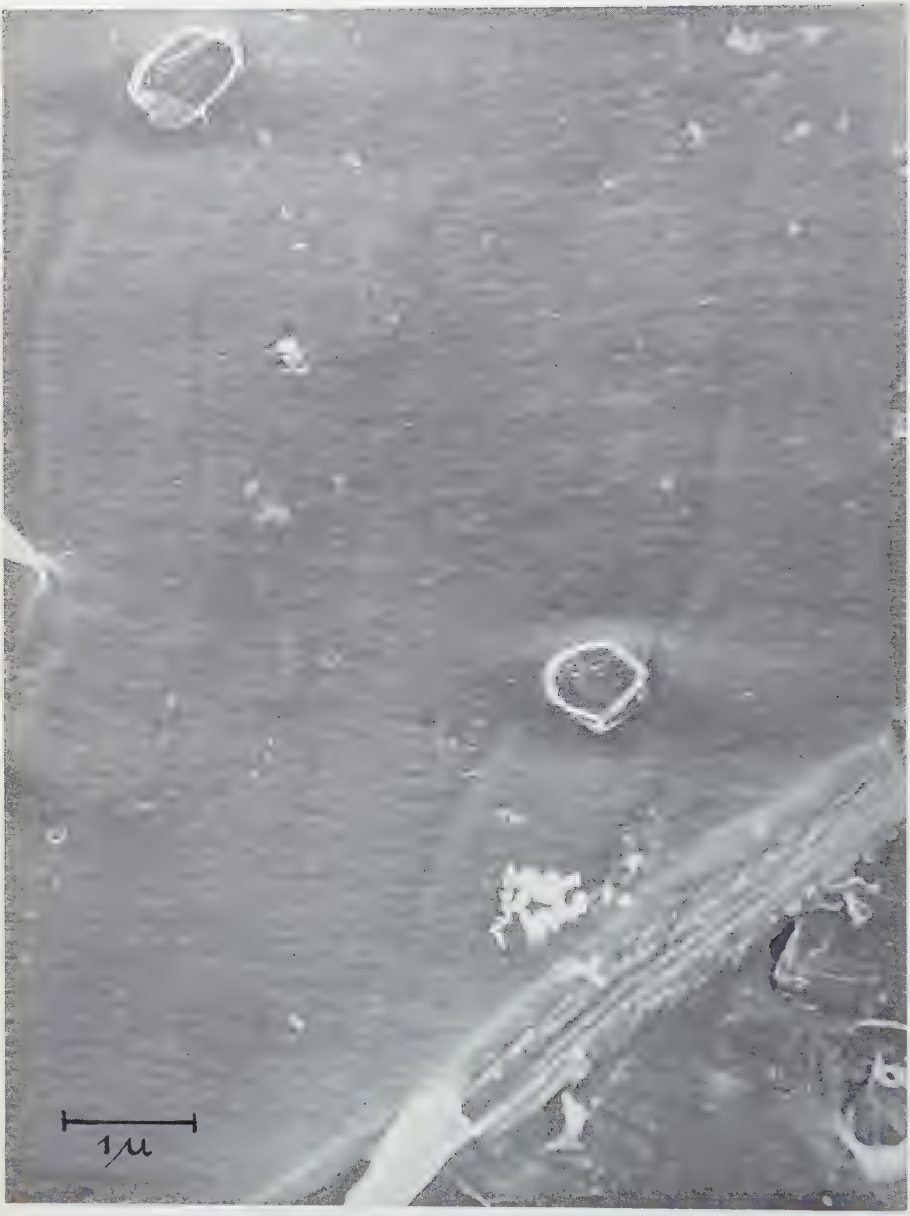

Fig. 10. Electron micrograph (replica) of a cross-section of a parenchyma cell. The replica film that covered the wall layer adjoining the lumen, is visible. Two pits with plasmodesm openings. Magnification 17000 ×

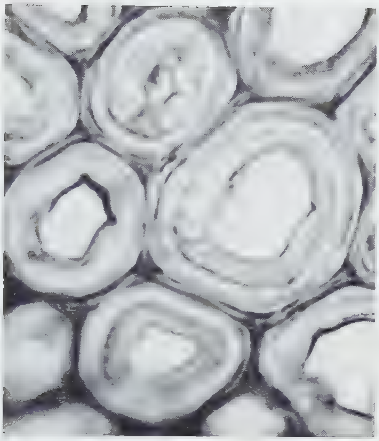

Fig. 6. Cross-section of fibres in the stalk of sugar cane swollen in H_2SO_4 62 %. Magnification 1150 ×

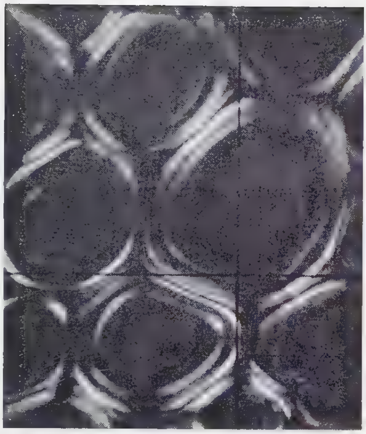

Fig. 8. The cross-section of Fig. 6 in polarized light between crossed nicols. Magnification 1150 ×

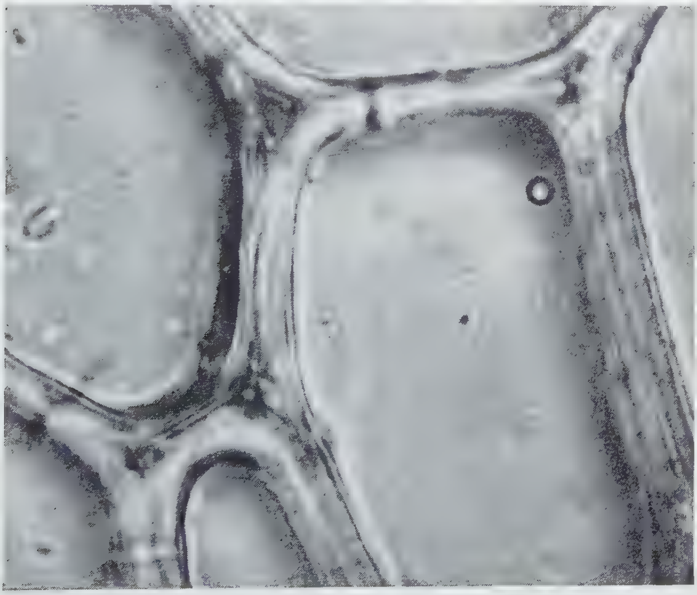

Fig. 7. Cross-section of parenchyma cells in the stalk of sugar cane (non-treated)

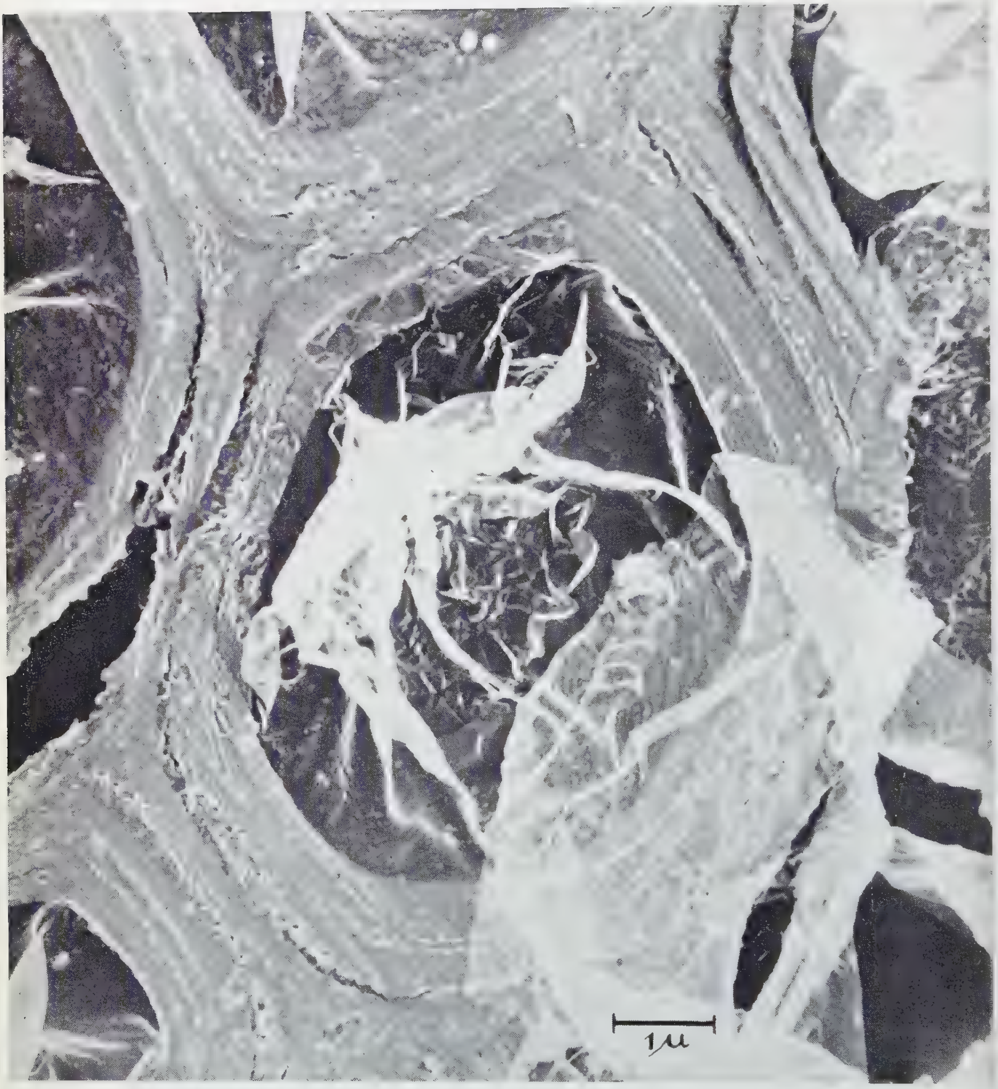

Fig. 9. Electron micrograph (replica) of a cross-section of a fibre (sugar cane). Magnification 12500 ×

As mentioned above, telescoping phenomena have also been observed in the fibres of bamboo, e.g. of the genus of *Melocanna*.

Preston and Singh (1950) stated that the spirals in which the cellulose chains are orientated, are generally steeper in the same ratio as the quotient $\frac{\text{cell length}}{\text{cell width}}$ is greater. Hence the swelling anisotropy of the successive layer parts is smaller in the fibres than in the sclereids and parenchyma cells. In accordance with this statement it appears from our investigations that in sugar cane the telescoping phenomena cannot be observed in the long, very thin fibre type, but in the long, thicker type. Most frequently the phenomenon can be seen in parenchyma cells and sclereids, and in the fibres of the short, spool-shaped type.

Summarizing, in sugar cane the structure of the cell wall of the described cells may be as follows: The secondary wall consists of layers which, as regards their network of cellulose, do not cohere, while the network of one wall layer forms a cohering whole. The chain molecules of all parts of the cell wall have a Z-spiral orientation. In the outer part (morphogenetically in the beginning) of each wall layer the spiral is more or less flat. Towards the centre (morphogenetically as the layer becomes thicker) the spiral becomes steeper.

The inner parts of the layers give the dark rings in the cross-sections between crossed nicols. In these parts the spiral of orientation, therefore, forms an angle with the cell axis of probably not more than about 10°.

The outer parts of the layers form the light rings in the cross-sections between crossed nicols. Here the angle in question must be considerably greater.

In the cells with a positive birefringence the beginning of a wall layer, i.e. the outer part of it, probably has an orientation spiral whose direction makes an angle with the cell axis smaller than 45°.

In the isotropic cells the angle referred to must be, in the beginning of a layer, greater than 45°. This spiral becomes gradually steeper.

In the cells with a negative birefringence the angle in question must be, in the beginning of a layer, considerably greater than 45°. This spiral becomes steeper but very slowly.

Whereas in the pulp the layers of the cell wall lie loose, these layers will cohere in the intact wall. The coherence may be caused by pectin, lignin or hemicelluloses. The latter do not come into account here, because they dissolve only partly during the pulping process. Pectin on the other hand dissolves completely during this process, and lignin for the greater part. By the following bleaching process lignin disappears almost entirely. In unbleached pulp telescoping phenomena occur sporadically, in non-treated tissues never. It is therefore concluded that the layers of the cell wall are connected with each other by pectin or lignin, or by both.

It might be taken into consideration that apart from a difference in orientation of the cellulose chains, the swelling anisotropy may be caused by alternating layers of cellulose and layers of a different chemical composition. This hypothesis cannot, however, be held for the following reasons.

If the dark rings in the cross-sections between crossed nicols were due to cellulose (with a steep spiral structure), the light rings would be caused by a strongly birefringent substance of a different chemical composition, which is more or less transversely oriented. Such a cell-wall substance is, however, not known. Pectin which sometimes shows a very small double refraction (Roelofsen and Kreger, 1951 and 1954), is no longer present in pulp.

The bright rings in the cross-sections should, therefore, be due to a cellulose layer (with a more or less transverse orientation). But then the dark rings may only be attributed to non-birefringent hemicelluloses which are present in the stalk of sugar cane in a rather large quantity (T.A.O. Forestry and Forest Products Study, 1953). This would not seem to be impossible, but then the telescoping phenomena should not occur after extraction of the hemicelluloses with 6,5 % NaOH according to Heuser, which apparently was not the case.

The swelling anisotropy of the inner and outer part of a wall layer may also be caused by a different degree of crystallization, this being high in the outer part and low in the inner. This supposition, the investigation of which is probably impossible, is contradicted by Fig. 10 showing an inner part of a layer in a highly fibrillized condition. Since it must be assumed that the fibrils consist of parallel oriented cellulose molecules, we hardly can think that the cellulose in certain fibrils may be non-crystalline and in identical ones crystalline.

If any given fibre swells in cuprammonium and forms beads as a result of a difference in orientation direction of concentric parts of the cell wall, the question arises of what may prevent the outer part of the cell wall from swelling in longitudinal direction. In swelling the cell does not elongate but, on the contrary, often shortens. This problem has hardly attracted attention but would perhaps be worth while further investigation.

The same applies to each cell-wall layer which forms part of the "composed wall" of fibres and of other elements in the stalk of sugar cane. The idea of the structure of that composed wall as developed above, may give a solution of the question. In the foregoing it has been suggested that the cellulose network of one cell-wall layer forms a cohering whole. This coherence of the network of cellulose chains will prevent the peripheral part of the wall layer from extending in longitudinal direction. The following phenomenon gives a nearer verification of this theory.

When in a fibre of sugar cane swelling in cuprammonium, beads have been formed and the beads are dissolved in the liquid, the intermediate "cuffs" keep floating for a considerable time. When these cuffs finally dissolve too, they always do so from inside and shockwise. It is seen that, all at once, one of the concentric cuffs extends to a high degree (like a compressed spring that is loosened) and then disappears, i.e. dissolves so suddenly. The outer part of a layer in a cuff tends to extend highly in longitudinal direction, but is prevented from doing so: its cellulose fibrils or micelles tend to swell and form separate hydrated chain molecules, but they are everywhere connected with the cellulose network of the inner part of the layer that "no longer gives way". As soon as, from the lumen, enough cellulose of the inner part of that layer is dissolved that the outer part is no longer restrained, the latter can give in to the tension in longitudinal direction caused by the swelling, and will suddenly extend to a high degree.

ACKNOWLEDGEMENTS

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SUMMARY

From the observations the following conclusions can be drawn:

1. The cell walls of the fibres, parenchyma cells, and sclereids in the stalk of sugar cane principally have the same structure.
2. The cell wall consists of several concentric layers.
3. The cellulose chains have a Z-spiral orientation in all layers.
4. In each layer of the cell wall the cellulose forms a cohering network.
5. The orientation direction of this network in the inner part of each layer is always steeper than that in the outer part.
6. The various layers are not connected by cellulose chains and, after the chemical pulping process, come to lie somewhat loose.
7. The cohesion of the cellulose network prevents the outer part of a layer in a swelling cell wall from extending in longitudinal direction as long as the inner part of that layer is still intact.

RÉSUMÉ

Les conclusions suivantes peuvent être déduites des observations décrites ci-dessus:

1. Les parois cellulaires des fibres, des cellules de parenchyme et des scléréides dans le tige de canne à sucre ont principiellement la même structure.
2. La paroi cellulaire se compose de plusieurs couches concentriques.
3. Dans toutes les couches les chaînes de cellulose ont une orientation en forme de spirale en Z.
4. Dans chaque couche de la paroi cellulaire la cellulose forme un treillis cohérent.
5. La direction d'orientation de ce treillis dans la partie intérieure de chaque couche est toujours plus raide que celle dans la partie extérieure.
6. Les couches diverses ne sont pas jointes par des chaînes de cellulose; après la lessivage du tissu ces couches sont détachées un peu.
7. La cohésion du treillis de cellulose empêche la partie extérieure d'une couche dans une paroi cellulaire dilatante de s'étendre dans la direction longitudinale aussi longtemps que la partie intérieure de cette couche est intacte.

ZUSAMMENFASSUNG

Aus den oben beschriebenen Wahrnehmungen können folgende Schlüsse gezogen werden:

1. Die Zellwände der Fasern, der Parenchymzellen und der Sklereide im Stengel von Zuckerrohr haben grundsätzlich die gleiche Struktur.

2. Die Zellwand besteht aus einigen konzentrischen Schichten.
3. Die Zelluloseketten sind in allen Schichten gemäss Z-Spirale orientiert.
4. In jeder Zellwandschicht bildet die Zellulose ein koherentes Netzwerk.
5. Die Orientierungsrichtung dieses Netzwerks ist im inneren Teil jeder Schicht durchwegs steiler als im äusseren Teil.
6. Die verschiedenen Schichten sind nicht durch Zelluloseketten verbunden und kommen nach dem Aufschliessen des Gewebes einigermassen gesondert zu liegen.
7. Der Zusammenhang des Zellulosenetzwerks verhindert den äusseren Teil einer Schicht in einer quellenden Zellwand sich in longitudinaler Richtung auszudehnen, solange der innere Teil dieser Schicht noch intakt ist.

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WAVELENGTH DEPENDENCE ON PHOTOPERIODIC RESPONSES

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In a previous paper it was reported that the effect of a long day treatment on the flowering response of some plant species is controled by at least two photoreactions (Meijer 1957). One of them is the nightbreak reaction for which a maximum of activity in the red part of the spectrum has been found. The effect of a red irradiation can be reversibly antagonised by a near infra-red irradiation given immediately after the red irradiation (Borthwick e.a., 1952). The other photoreaction takes place during the main light period. Stolwijk e.a. (1955) has found that *Hyoscyamus niger*, a long day plant, needs violet, blue or infra-red irradiation during the main light period of a long day treatment to obtain flowering. In a long day in green light no flowering occurred, whereas in red light flower initiation was retarded.

The same blue or infra-red necessity to obtain a long day effect has also been found for some other plants, f.i. *Salvia occidentalis* a short day plant, *Petunia*, *Arabidopsis thaliana*, *Plantago major*, lettuce and *Silene armeria*, all long day plants (Meijer, 1957).

The influence of the light quality of the main light period on the effect of a short day treatment of *Kalanchoë blossfeldiana*, a short day plant, was studied by Wallrabe (1943). She concluded that a short day in green light is not effective in inducing flowering. A short day treatment in blue light is more effective than the same treatment in red light.

In this paper experiments are described to give some more information about the influence of the light quality of the main light period on photoperiodic responses.

METHODS AND MATERIAL

The experiments were carried out in the plant growth cabinets described by Van der Veen (1950), the characteristics of the light have been given by Meijer (1957), Fig. 1. The day temperature was 22° C., the night temperature 17° C. The effect of a short day treatment on flowering was studied in experiments with the short day plants *Kalanchoë blossfeldiana* and *Salvia occidentalis*. *Larix leptolepis* was used to see whether there is an influence on the induction of winter dormancy or not.

The influence of the light quality for a main light period of 10 hours combined with a night break of 10 minutes with coloured light has been studied in experiments with an annual strain of *Hyoscyamus niger* var. *pallida* and with *Salvia occidentalis*, respectively a long day and a short day plant.

EXPERIMENTAL RESULTS

1. *Short day experiments*

Kalanchoë, *Salvia* and *Larix* were grown in a glasshouse in a long day of at least 16 hrs. light per day. During the experiments plants were given a short day treatment of 10 hrs. light per day in red, green and blue light during 2, 4, 6, 8, 10, 12, 14 or 16 days. After the treatment each group of plants was kept in the glasshouse in a long day.

The light intensities for the red, green and blue light are respectively 950, 880 and 900 μW/cm^2.

Salvia

At the beginning of the treatment the youngest leaf pair of *Salvia* plants was marked and at the end of the experiment the number of new formed leaf pairs was counted. A treatment of 16 short days in red, green and blue light was necessary for the induction of a terminal inflorescence. The average numbers of leaf pairs formed before the inflorescence appeared are respectively 6.5, 6.5 and 5.5 for the plants treated with red, green and blue light. A treatment of 10 short days or less in red and blue and of 8 short days or less in green light did not have a flower inducing effect at all. At the end of the experiment these plants had formed 10, 10.5 and 10 leaf pairs in red, green and blue light respectively. A short day treatment of 12 and 14 days in red and blue light and of 10, 12 and 14 days in green light showed a slight indication of flower induction; one or two bract-like leaves were formed after which the development of normal leaves was continued. The number of new formed leaf pairs up to the first bract-like leaf was 6 in red, green and in blue light.

Kalanchoe

In *Kalanchoe* a short day treatment of at least 6 days in red and green light and of at least 8 days in blue light induced the initiation of flowerbuds. There was hardly any difference in the time after which the flower buds were macroscopically visible. These results are contrary to those of WALLRABE (1943) who found that *Kalanchoe* did not initiate flowers in short days with green light.

Larix

In previous experiments in white light, it has been shown that *Larix* is very sensitive to a short day treatment. About 7 short days of 10 hrs. light per day are already sufficient for the initiation of a terminal bud, which appears in about three weeks after the beginning of the treatment. Some time afterwards this bud resumes growth again in long days. The duration of this induced dormancy period of the terminal bud depends on the length of the preceding short day treatment. A treatment of less than 7 days gave a slight indication of induction. Only a number of scale-like needles are formed, but growth is not stopped and after this brief intermezzo the formation of normal needles is continued. 23 days after the beginning of the treatment all plants treated during 10—16 days in red and green light and during 8—16 days in blue light showed a terminal bud. A treatment of two short days did not have any effect, whereas 4 and 6 short days in red light and 4 short days in blue and green light induced a number of scale-like needles. The plants treated with 6 short days in blue and green light and 8 short days in red light formed partly a terminal bud and partly only a number of these scale-like needles. The duration of the dormancy period of the terminal bud did not show any difference between plants induced in red, green or blue light.

2. *Night break experiments*

In another series of experiments, *Salvia* and *Hyoscyamus* plants were treated during respectively 16 and 37 days in red, green and blue light during 10 hrs. per day. Of each group some plants were irradiated during 10 minutes in the middle of the dark period with red, green or blue light, whereas an other part was kept in darkness during this time (control plants). The light intensities for red, green and blue light were respectively 900, 850 and 950 $\mu W/cm^2$ for the main light period as well as for the light used as a dark interruption. The results are given in table I and II. Both plant species reacted

Table I

The influence of the light quality of a main light period of 10 hrs. per day and of a dark interruption of 10 minutes on the flowering response of *Salvia occidentalis* (S. D. plant). Duration of the treatment: 16 days. Stage of the growing points 58 days after the beginning of the treatment. + = generative, — = vegetative. Number of plants 4.

night break main light period	control	10′ red	10′ green	10′ blue
10 hrs red	+ + + +	— + + +	+ + + +	+ + + +
10 hrs green	+ + + +	+ + + +	+ + + +	+ + + +
10 hrs blue	+ + + +	— — — —	— — — —	+ + + +

Table II

The influence of the light quality of a main light period of 10 hrs. per day and of a dark interruption of 10 minutes on the flowering response of *Hyoscyamus niger* (L. D. plant). Duration of the treatment: 37 days. Stage of the growing points 37 days after the beginning of the treatment. + = generative, — = vegetative. Number of plants 3.

night break main light period	control	10′ red	10′ green	10′ blue
10 hrs red	— — —	— — —	— — —	— — —
10 hrs green	— — —	— — —	— — —	— — —
10 hrs blue	— — —	+ + +	+ + +	— — —

very uniformly and it is very clear from these results that a long day effect can only be obtained when the plants receive blue light during the main light period and red or green light during the night break.

The *Hyoscyamus* plants grown in 10 hrs. blue light + 10′ red started bolting 10 days after the beginning of the treatment and at the end of the treatment flower buds were macroscopically visible. In 10 hrs. blue light + 10′ green no elongation of the stem was obtained even at the end of the experiment; flower buds however were microscopically visible at that time. In all other treatments plants remained vegetative.

Discussion

The experiments described in this paper indicate:

1° That the effect of a short day treatment is not much influenced by the quality of the light for the species used.

2° That the night break is only effective if the light given during the main light period contains blue radiation (or perhaps infra-red, which was not investigated in these experiments).

In a previous paper we concluded that for some short day and long day plants a long day treatment was effective only when the light given during this long day contained blue or infra-red radiation (Meijer 1957). This is in accordance with the experiments with *Hyoscyamus* of Stolwijk (1955).

It seems therefore that in order to induce a long day effect, a plant needs either a few hours of blue (or perhaps infra-red) irradiation and afterwards, as a night break red light, or the long day effect can be obtained by giving long days with blue or infra-red. In these last conditions red light is not at all necessary. So in the first case the plant needs blue and red, in the second only blue to show the long day reaction.

One explanation for this behaviour may be that blue light has still some activity when given as night break light, although much less than red. (Borthwick e.a., 1948) During the 16 hours illumination, which might be considered as a short day of 10 hours and an additional 6 hours, the last few hours may act as night break light. A few hours of blue night break light could possibly be as active as 10 minutes of red and therefore change the short day into a long day.

Another possibility is that in the blue long day the necessity for red is fulfilled by the fluorescence of the chlorophyll in blue light. A green plant can never be exposed to pure blue or green light only, because 1 to 0.1 % of the light absorbed is transformed into red + infra-red fluorescent light by the plant itself. This red fluorescent light might act as night break light during the last hours of the long day in blue.

It must be mentioned here that *Kalanchoe* and also *Euphorbia pulcherrima* did not flower and that *Larix* did not show any sign of dormancy when these plants are grown in 16 hours green light per day. The green used still contained a trace of red (Meijer, 1957; Fig. 1) and the fluorescence of the chlorophyll emits red and infra-red radiation. Therefore it may be possible that for some very sensitive plants the need for infra-red and for red may have been sufficiently satisfied by a long day exposure to green light.

Of course these explanations must be considered as tentative. The subject is under further investigation.

SUMMARY

It has been shown in several plants that the effect of a short day treatment does not depend on the light quality of the main light period. However to obtain a long day effect by interrupting the long night period with a red or green irradiation it has been shown that a special blue light requirement for the main light period exists.

ACKNOWLEDGEMENT

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PHOTOSYNTHETIC PHOSPHORYLATION AS AN EXPLANATION FOR INDUCTION PHENOMENA IN PHOTOSYNTHESIS

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1. Introduction

When green plant material is brought from darkness into light, photosynthesis in general does not immediately start at full rate; in most plants some time is needed for the adaptation from the dark to the light state. During this period photosynthesis may increase in some cases continuously, in others the steady state rate is reached only after one or more oscillations.

Aufdemgarten (1939) and Van der Veen (1949) measured these induction phenomena with a diaferometer [1]), and observed with some plants a particular phenomenon which they called "initial uptake": at the onset of illumination, the rate of CO_2 uptake rises sharply for about 15 seconds, then it decreases more or less sharply, then rises again more slowly and after several minutes eventually reaches the steady state level, often after one or two further and slower oscillations. The initial uptake was quite independent of the rest of the adaptation process and in some respects of the steady state level of photosynthesis: at a temperature of 1 to 2°C photosynthesis was slowed down almost to zero rate, but the initial uptake was hardly smaller than at 20°C. When the leaf was kept in water of about 45°C for some minutes prior to the measurement, photosynthesis was completely inhibited, whereas the initial uptake was not impaired. In this case, a gush of CO_2 was observed at the end of the illumination period which was the reverse of the initial uptake. In normal leaves the dark level of CO_2 release (dark respiration) is reached at once and without any oscillations at the end of illumination. Fig. 1 shows adaptation lines which display these phenomena schematically.

An explanation of these adaptation phenomena may be found in changes of steady state concentrations: in a living tissue which metabolizes under given, constant external conditions, the concentration of each metabolite assumes a certain value, such that the rates of the reactions by which the compound is formed balance the rates of the reactions by which it is transformed. If the external conditions are suddenly changed, some reaction rates will change too; the concentrations then have to assume a new value in order to come into equilibrium with the new reaction rates. As, in general, a reaction rate is dependent on the concentration of the reactants, the rates will continue to change so long as the concentrations of the metabolites are not constant.

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[1]) The diaferometer is an instrument by which the concentration of CO_2 in the air which has passed through a small photosynthetic chamber is measured continuously by means of the heat conductivity of the air. This property is much more dependent on the concentration of CO_2 than of O_2.

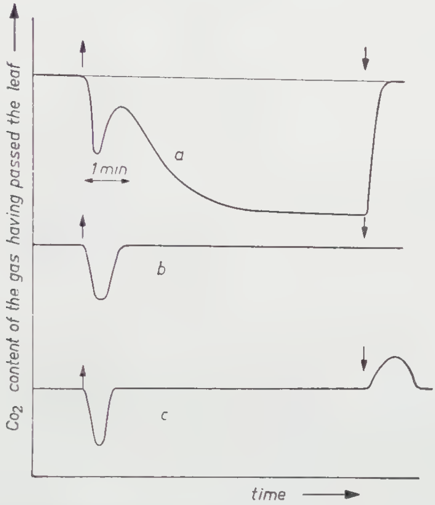

Fig. 1. Adaptation lines showing the initial uptake schematically (from VAN DER VEEN (1949). *a*) normal leaf at room temperature; b) normal leaf at 2°C; c) heat treated leaf, at room temperature; ↑ begin, ↓ end of illumination period.

The work described here was undertaken with the aim of finding the reactions which give rise to the induction phenomena of photosynthesis, and especially to the initial uptake.

2. MATERIALS, METHODS AND RESULTS

With different plants, very different induction curves can be obtained after the transition from dark to light. Whereas some plants show a very marked initial uptake after short dark periods (5 to 30 minutes), other plants do not show it at all: upon illumination, the rate of CO_2 uptake increases gradually or with some very slow oscillations and reaches the steady state value after 5 to 10 minutes. Furthermore one plant displaying for some time a marked initial uptake may suddenly fail to do so. The occurrence of this phenomenon is probably dependent on certain culture conditions or on the nutritional state of the plant. AUFDEMGARTEN (1939) describes such an effect: the green alga *Stichococcus bacillaris* shows a strong initial uptake when cultivated in Eiler solution but fails to do so in Kolkwitz solution.

The unicellular alga *Scenedesmus* shows no initial uptake at all under the conditions of the diaferometer and has a very short induction time; photosynthesis reaches its full value within 30 seconds. When the suspension of algae is heated to 47° C prior to the measurement, photosynthesis is almost completely stopped, but sometimes a faint initial uptake can be observed.

Most of the work described here has been done with leaves of *Dahlia* (a horticultural variety) and of *Datura arborescens* grown in the garden. The *Datura* tree was covered with a collapsible hot house during the cold months.

The changes of the concentrations of the intermediate products of photosynthesis during the transition from the dark to the light state were studied by means of CO_2 labelled with the radioactive isotope C^{14}. The set up was similar to the one used by CALVIN and MASSINI (1952) for the measurement of metabolite concentrations.

12 rectangular pieces of *Dahlia* leaves, 10 by 50 mm, were arranged in a flat rectangular perspex vessel in a plane parellel to the double walled windows of the vessel. Each piece was mounted in a frame which could very quickly be pulled out of the vessel.

Between the parallel window panes water of constant temperature circulated. The vessel was included in a closed system consisting of a gas circulating pump of the rubber tubing type, a reservoir vessel of 3 l volume containing a mixture of air with 1 % radioactive CO_2 (about 0.2 mc/mmol), a flask for the generation of the CO_2 from radioactive $BaCO_3$ and two traps filled with a 1-n solution of NaOH to trap the CO_2 not used during the experiment. The perspex vessel was illuminated through its two windows by two banks of sodium vapour discharge lamps providing a light intensity of 4500 μW/cm². The cooling water was kept at 20°C.

The leaf pieces were cut from freshly harvested leaves and mounted in the frames of the illumination vessel. Then they were allowed to assimilate for 15 minutes the radioactive CO_2 generated previously and mixed with the air in the reservoir vessel. During this time the intermediate products of photosynthesis were so thoroughly labelled with C^{14} that they acquired a constant activity. At this moment the perspex vessel was darkened for 10 minutes, then illuminated again. During the last minutes of the first illumination and of the dark period, and during the first minutes of the second illumination period the leaf pieces were successively withdrawn from the vessel and immersed in chilled alcohol containing 1 % acetic acid, then ground and extracted successively with 80 % alcohol, 30 % alcohol and finally with water. The extracts were concentrated in vacuo and the soluble compounds separated by means of two dimensional paper chromatography (BENSON, *et al.*, 1950) using n-butanol-acetic acid-water 4:1:5 as first solvent and phenol, saturated with phosphate buffer of pH 7.5 (LEVY and CHUNG, 1953) as second solvent. The radioactive spots were detected by means of autoradiography on X-ray film and counted directly on the paper with a large area end window Geiger-Müller tube.

As the intermediate products had acquired a constant activity during the first illumination period, the radioactivity contained in a compound on the chromatogram was a direct measure of its concentration at the moment the cells were killed. In this experiment the concentration of the phosphorylated intermediate products of the photosynthetic cycle (carbohydrate phosphates and phosphoglyceric acid, (see BASSHAM *et al.*, 1954) were very low during illumination, dropped to $^1/_3$ in the dark and reached the light value again within 1 minute upon re-illumination. The steady state concentration of all the phosphate esters together in the light was about 0.1 μmoles/g fresh weight. In two similar experiments made with the unicellular alga *Scenedesmus* this value was about 1 μmole/cc wet packed algae. The concentration of malic acid was in the light also about 0.1 μmoles/g. It dropped to $^1/_2$ this value in the dark but recovered within 15 seconds of light.

In order to check whether the CO_2 fixed during the initial uptake is incorporated into a stable compound, the rate of incorporation of radioactive C in light was measured without prior saturation of the photosynthetic reservoirs with C^{14}. It turned out that the photosynthesis of normal leaves was so high compared to the initial uptake, that the latter could hardly be expected to rise above the background of photosynthesis in the time curve of fixation of C^{14} in light. An experiment was therefore performed with 3 pieces of *Datura* leaf treated at 46° C for two minutes, in order to depress photosynthesis without affecting the initial uptake.

The pieces were mounted in a flat glass vessel incorporated in a closed gas circulating system in such a way that they could be illuminated in a constant temperature bath, and at a given moment could be flooded with a cold mixture of ethanol-formic acid-water 10:1:9. In the gas system a reservoir containing $C^{14}O_2$ and a trap filled with a 1-n solution of NaOH as well as a circulating pump were incorporated. The first sample was killed after one minute dark in an atmosphere containing $C^{14}O_2$; the second was killed in the light after one minute dark with $C^{14}O_2$ and 10 seconds light; the third after one minute dark, 10 seconds light and one minute dark. The samples were cooled to 0°C immediately after killing, extracted with the killing mixture and centrifuged in the cold. The radioactivity of the extracts was then measured by evaporating an aliquot on an aluminum disc and counting the disc with a Geiger–Müller tube.

TABLE I

Radioactivity fixed by leaf pieces of *Datura*, treated at 46°

	treatment	cpm in extract
1	1 min dark	390
2	1 min dark – 10 sec light	710
3	1 min dark – 10 sec light – 1 min dark	780

The results of this experiment are listed in table I. On another piece from the same leaf, treated in the same manner at 46° C, the induction curve was determined in the diaferometer. This piece consumed 0.15 mm³ CO_2 during the initial uptake, which corresponds to 1400 counts per minute for the specific activity of the CO_2 used. It is clear that the CO_2 consumed during the initial uptake was not incorporated into a stable, extractable compound.

The dependence of the initial uptake and of steady state photosynthesis on the light intensity was measured in the diaferometer with *Datura* leaf pieces. Fig. 2 shows that the initial uptake is saturated at a light intensity which is much lower than the saturating intensity of photosynthesis.

The action spectrum of the initial uptake of heat treated leaves of *Impatiens* was determined roughly by isolating different spectral regions by means of Schott filters. Blue and green was slightly less active than red and yellow. This is in qualitative agreement with the action spectrum of photosynthesis.

The dependence of the initial uptake on the concentration of CO_2 was investigated by means of the diaferometer with leaves of *Dahlia* in air containing 0.03 to 20 % CO_2. Fig. 3 shows that the amount of CO_2 consumed during the initial uptake increases to a much greater extent with increasing CO_2 concentration than photosynthesis does.

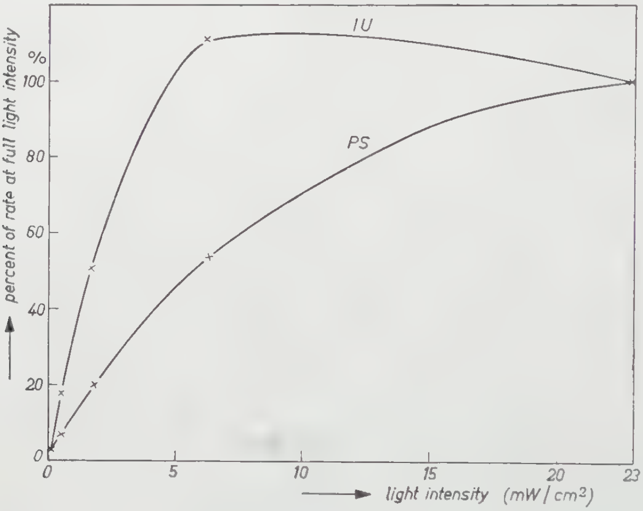

Fig. 2. Light saturation curve of initial uptake and photosynthesis, *Datura*. I U = maximum rate of initial uptake after 10 min. dark; PS = steady state rate of photosynthesis; temperature = 20°C; 3 % CO_2 in air.

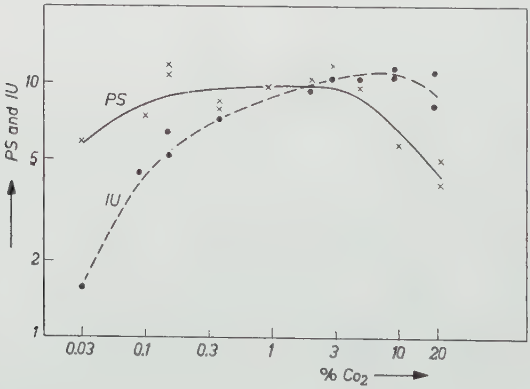

Fig. 3. CO_2-saturation curve of initial uptake and photosynthesis, *Dahlia*. I U = amount of CO_2 consumed during initial uptake per leaf piece after 10 min. dark, relative units; PS = steady state rate of photosynthesis, relative units; temperature = 20°C; light intensity = 23 mW/cm².

The influence of a series of inhibitors on photosynthesis and on the initial uptake is shown in Table II.

Leaf pieces of *Datura*, *Dahlia* or *Impatiens* were allowed to float on the solution of the inhibitor for 2 to 8 hours. A control piece was placed on distilled water for the same time. The induction curve was then measured with the diaferometer. Infiltration of the pieces in vacuo resulted in the disappearance of the initial uptake even with water, probably because the clogging of the internal gas spaces of the leaf caused a much slower diffusion of the CO_2 and therefore a more sluggish response of the gas phase to reactions taking place in the liquid phase of the leaf.

TABLE II

Influence of inhibitors on photosynthesis and initial uptake. For explanation see text.

Inhibitor	conc.	time of inhibition hours	plant	% inhibition	
				PS	IU
o-phenanthroline	10^{-3} – m	2	*Datura*	50	50
hydroxylamine	10^{-2} – m	2	*Dahlia*	55	50
phenyl-urethane	10^{-3} – m	2	*Dahlia*	60	40
2,4 – dinitrophenol . . .	10^{-3} – m	2	*Dahlia*	60	40
N-p-chlorphenyl–N′N′-dimethylurea	10^{-5} – m	5	*Impatiens*	60	45
iodoacetamide	10^{-3} – m	2	*Dahlia*	50	0
	10^{-2} – m	2	*Dahlia*	95	0
	10^{-2} – m	5	*Dahlia*	100	30
	10^{-3} – m	5	*Datura*	50	0
	5.10^{-2} – m	2	tomato	60	0
aminophenyl-dichloroarsine	10^{-3} – m	5	*Dahlia*	35	60
K-p-chloro-mercuribenzoate	5.10^{-4} – m	5	*Dahlia*	25	15
malonate	up to 0.1 – m	6–8	*Datura*	little effect	
NaF.	up to 10^{-2} – m	3	*Dahlia*	little effect	

Most inhibitors of photosynthesis inhibit the initial uptake also, with the exception of iodoacetamide which affects it much less.

Malonate was tried because the first experiment with labelled CO_2 suggested the possibility that the CO_2 consumed during the initial uptake was fixed into malic acid. Malonate is known to inhibit this reaction (DAS, 1937); it was found however that this compound has little effect on both the initial uptake and on photosynthesis.

DISCUSSION

If we wish to consider the possible reactions which could give rise to the initial uptake we will have to look first into the photosynthetic cycle proper, the conversion of carbon dioxide to carbohydrates.

According to BASSHAM *et al.* (1954) the only step of the cycle where CO_2 is consumed is the carboxylation of ribulose diphosphate. The reaction product is split into two molecules of phosphoglyceric acid. The carboxylation is catalyzed by the enzyme carboxydismutase and is independent of light (QUAYLE *et al.*, 1954 and WEISSBACH *et al.*, 1954)· The light energy absorbed by chlorophyll is converted into the chemical energy necessary for the reduction of phosphoglyceric acid to triose phosphate. Part of the energy, however, is converted into the free energy of hydrolysis of the "high-energy phosphates" such as adenosine di- and triphosphate (ADP and ATP), which is partly used to keep the photosynthetic cycle turning. (A survey of the role of high-energy phosphates in photosynthesis is given by ARNON, 1956.)

If the CO_2 consumed during the initial uptake is incorporated into ribulose-diphosphate, then light must influence this reaction indirectly, either by supplying the substrates or by removing the products of the carboxylation reaction. Both assumptions are rendered improbable in the light of the experiments described above. The reaction by which the products are removed is the reduction of phosphoglyceric acid. This reaction is inhibited strongly by iodoacetamide (MEYERHOF and KIESSLING, 1935), whereas the initial uptake is not affected at a concentration where photosynthesis is strongly inhibited (see Table II). If the substrates for the carboxylation are supplied by a light dependent reaction, then the product of carboxylation, phosphoglyceric acid, should accumulate during the first minute after illumination. This was not the case according to the first experiment described where the intermediates were saturated with C^{14} and their concentration measured during the adaptation period. Only traces of phosphoglyceric acid could be detected during the whole experiment.

Phosphoglyceric acid which is a stable and alcohol soluble compound should also have been present in the extract of a leaf which has consumed radioactive CO_2 in the light, according to the experiment summarized in table I. This experiment points to the possibility that the CO_2 is not incorporated into an organic compound at all but is converted into bicarbonate ions dissolved in the cell sap. According to the "Henderson-Hasselbach equation"

$$\log \frac{(HCO_3^-)}{(CO_2)} = pH - pK$$

(see UMBREIT *et al.*, 1954), the concentration of bicarbonate ion is directly connected with the pH so long as the concentration of dissolved CO_2 remains constant owing to the equilibrium with the CO_2 in the gas phase, and a shift of the pH toward alkalinity causes a conversion of CO_2 to bicarbonate ion. This is followed by an uptake of CO_2 from the gas phase according to the equation

$$OH^- + CO_2 \rightleftarrows HCO_3^-.$$

The extent of the uptake is roughly proportional to the concentration of the CO_2 in the gas at a given pH. At the high concentration used in the diaferometer experiments a very small change in the pH is sufficient for an appreciable conversion of CO_2 into HCO_3^-, as can be shown by calculation: if the pH of 1 cc solution which is in equilibrium with a gas phase containing 3 % CO_2, changes from 7.0 to 7.1, then 1 μmole CO_2 passes from the gas to the solution. In comparison, the amount of CO_2 consumed during the initial uptake is of the order of 0.2 μmoles/g leaves, fresh weight. Fig. 3 shows that the initial uptake is much more dependent on the concentration of CO_2 than photosynthesis is. This is in agreement with this hypothesis.

CHRIST (1955) measured electrical potentials between the roots and an illuminated leaf of *Pelargonium zonale.* At the moment of illumination the potential difference rises sharply, then decreases again and reaches a steady state value after about 40 min. in a manner similar to the curves obtained with the diaferometer. Although it is very difficult to interpret the physical meaning of those potential differences in such a complicated electrochemical chain it is conceivable that the changes in potential difference reflect a change in the pH of the cell content at the transition from dark to light.

Some aspects of the initial uptake described by VAN DER VEEN (1949) and represented in Fig. 1, b and c suggest that it may occur independently of photosynthesis as a whole. A survey of the action of inhibitors (Table III) shows that under the three partial processes which together form photosynthesis, the photosynthetic phosphorylation rather than the photolysis of water or the CO_2 fixation contains the cause of the initial uptake. It is very probable that photosynthetic organisms form ATP and ADP from ADP and AMP respectively and inorganic phosphate (P_i) (ARNON,1956 and SCHWINCK, 1956). If this reaction proceeds at a pH of 7, about 0.7 moles of OH^--ion is formed per mole reactants (ALBERTY e.a. (1951)):

TABLE III

Survey of the action of different inhibitors

inhibitor	PL a)	PSP b)	CF c)	IU d)	PS e)
o-phenanthroline	+	+	+	+	+
2,4-dinitrophenol	(+)	+	+	+	+
KCN	—	+	+	+ f)	
K-p-chloromercuribenzoate	—	+	+	(+)	(+) g)
iodoacetamide	—	—	+	—	+

a, b and c according to ARNON *et al.* (1956)
a = photolysis of water
b = photosynthetic phosphorylation
c = CO_2 fixation
d and e measurements with the diaferometer
d initial uptake
e steady state rate of photosynthesis
f according to AUFDEMGARTEN (1939)
g the inhibition by p-chloromercuribenzoate was comparatively small, probably because of slow entrance of the inhibitor into the intact leaf.

$$ADP^{2-} + HPO_4^{2-} \rightleftarrows ATP^{3-} + OH^-$$

In the living cell the OH^--ions react partly with the buffering system which consists of proteins, amino acids, phosphates etc. If the amount of the phosphate which takes part in the reaction is an appreciable part of the whole buffering system, then a small increase of the pH, and hence an uptake of CO_2 from the gas, will result in spite of the buffering action. It is difficult to estimate the buffering capacity of the plant cells in vivo, also because the reaction may take place only in part of the cell volume or only in part of the cells of the tissue. But there is some evidence that the amount of energy-rich phosphates formed in light, especially during the first moments of illumination, is not negligible compared to the rest of the buffering system.

Unfortunately, most of the measurements of incorporation of phosphate which have been reported have been made with *Chorella*, an organism which does not display an initial uptake at all, and even gives off a gush of CO_2 at the onset of illumination. However, it should be pointed out that in spite of a fast phosphorylation in the light, an initial uptake will not occur if the pH in situ is such that no OH^-ions are formed during phosphorylation, or that the CO_2-carbonate system has no buffering capacity, or if the cell content is so strongly buffered that the pH shift is extremely small. It seems therefore not unreasonable to use the evidence with regard to light phosphorylation in *Chorella* in this connection.

Kandler (1950) found a quick decrease of the P_i-content of Chlorella in the first seconds of illumination; the decrease was of the order of 0.5 to 1 μmoles/cc wet packed algae. Wassink, Wintermans and Tjia (1951) illuminated a suspension of *Chlorella* in the absence or presence of CO_2 and also measured the decrease of the P_i of the cells after one to six hours. They found a strong decrease of P_i in the light when photosynthesis was inhibited by lack of CO_2, to an extent of up to 30 μ moles/cc wet packed algae per hour. As photosynthesis as a whole is inhibited in the first moments of illumination, it is possible that at this moment the formation of energy-rich phosphate too proceeds at an increased rate.

Strehler (1953) measured the formation of ATP in a suspension of *Chlorella* incubated anaerobically in the dark, upon illumination or upon admission of O_2 in the dark. He found that the production of ATP by illumination was comparatively little inhibited by low temperatures. This is in agreement with the slight inhibition of the initial uptake by low temperatures (see Fig. 1, b).

Schwinck (1956) found ATP also in leaves of *Elodea densa*, but could not detect it in extracts of *Spinacia* or *Viola* by means of paper chromatography because some substances present in the extract hindered a good separation.

Wessels (1957) measured the light-induced phosphorylation in a suspension of chloroplasts of spinach. He found a formation of ATP of up to 0.25 μ moles per minute in the chloroplasts isolated from 1 g leaves.

An incorporation of P_i into other compounds than adenosine nucleotides must also influence the pH of the cell content. Holzer (1951) found that a great part of the easily hydrolysable phosphates of *Chlorella* consists of metaphosphates. WINTERMANS (1954) detected an accumulation of polyphosphates in *Chlorella* during illumination. The incorporation of P_1 into polymeric phosphoric acids must be accompanied by an increase of the pH analogous to the formation of ATP. On the other hand, phosphorylation of e.g. glucose causes a decrease of the pH at pH 7. Glucose-1-phosphoric acid has a second pK of 6.5, compared to 7.2 for orthophosphoric acid (ASHBY *et al.*, 1955), so that, at pH 7, about 0.4 moles H^+ ion are formed per mole reactants for the reaction

$$\text{Glucose} + H_3PO_4 \rightleftarrows \text{glucose-1-phosphoric acid} + H_2O.$$

As this and similar reactions can only proceed at the expense of ATP, the rise of pH created by the formation of ATP must be reversed as soon as the ATP is used up for different phosphorylations. It is therefore quite possible that the initial uptake should be interpreted as a rapid sequence of a "gulp" and a "gush" of CO_2 superimposed on the slope of the CO_2 fixation curve caused by the increase in photosynthetic rate during the induction period.

The hypothesis presented for the origin of the initial uptake might also furnish an explanation of the inverse induction phenomenon, the so-called gush of CO_2 observed sometimes at the onset of illumination (for a review see RABINOWITCH, 1956). If the reactions using up ATP predominate over its formation, the pH of the cell content should decrease and therefore an evolution of CO_2 should result. However, in view of the observation of BROWN and WHITTINGHAM (1955) that o-phenanthroline does not affect the gush at a concentration where photosynthesis is almost completely inhibited, it is more probable that the gush has no connection with the photosynthetic phosphorylation.

SUMMARY

The initial uptake of CO_2 by photosynthetically active tissue after the transition from dark to light is investigated. It is suggested that this phenomenon is caused by a shift in the pH of the cell medium toward alkalinity which is due to the formation of energy-rich phosphates in the light.

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THE EFFECT OF LEAF AGE ON THE RATE OF PHOTOSYNTHESIS IN DETACHED LEAVES OF TREE SEEDLINGS

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INTRODUCTION

That the maximum rate of photosynthesis varies with age of the plant material is an assumption which has found its way into many text books of plant physiology (see e.g. 1,2). The experimental evidence offered in its support, however, is surprisingly meagre, and, in particular, data relating to tree seedlings are conspicuously deficient. Experiments recording a reduction in maximum rate of photosynthesis with age of cultures of unicellular algae have been reported by WASSINK and KATZ (1939) and PRATT (1943). Although it is often difficult to be certain that the effects observed with algal cultures are not due merely to "ageing" of the growth medium, PRATT (1940, 1943) has provided unassailable evidence of an ageing effect within the plant cells themselves by extracting an inhibitor of photosynthesis from aged *Chlorella* cells. For trees, evidence has been recorded by WILLSTÄTTER and STOLL (1918), who found a 100 % increase in maximum assimilation level between "young" and "old" leaves of both *Acer pseudoplatanus* and *Tilia cordata.* Expressed per unit of chlorophyll, however, the rate of assimilation showed a 60 % decrease from "young" to "old" leaves and the authors infer from this that a protoplasmic factor other than chlorophyll limits photosynthesis in old leaves. BRIGGS (1920) came to the same conclusion following experiments with etiolated seedlings, while DASTUR (1924, 1925) recorded similar effects in herbaceous plants, but found also that differences in photosynthetic activity run parallel with differences in water content of the leaves. He concluded that the limiting "internal factor" was water.

The present paper describes experiments in which the effect of leaf age on photosynthesis in various species of *Acer* and *Quercus* was studied. In an attempt to distinguish actual and physiological age, data were also obtained for plants grown under different daylength conditions.

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EXPERIMENTAL MATERIAL AND METHODS

Experiments were made with detached leaves of first year seedlings of the following species: — *Acer pseudoplatanus L.*, *A. platanoides L.*, *A. saccharinum L.*, *Quercus robur L.*, and *Q. borealis maxima* (MARSH) ASHE. With the exception of the daylength series, the plants were raised in gravel cultures (for details, see 10) under constant conditions of light intensity (5000 lux for 16 hours per daily cycle) and temperature (20° C ± 1.0° C). The daylength series comprised seedlings of *Acer saccharinum* which had been raised under different photoperiods. Plants from long-day (L.D.) conditions (24 hours of light per day) and having 9 leaf pairs, were compared with plants from a short-day (S.D. 10 hours of light per day) and having only 4 leaf pairs.

Carbon dioxide assimilation in relation to light intensity was measured by means of the diaferometer technique developed for botanical purposes by AUFDEMGARTEN (1939) and VAN DER VEEN (1949).

This technique involves the determination of changes in the composition of gas mixtures by measuring the corresponding changes in their thermal conductivity. Since the conductivity of CO_2 is less than that of air and that of O_2 is approximately the same as that of air, a change in the CO_2 content of air will change its heat conductivity; these changes can be measured with the diaferometer. The apparatus used in the present work has been described in detail by SPIERINGS *et al.* (1952). Briefly, a thin platinum wire is heated by a uniform electric current from a 6-volt battery, regulated by a rheostat. The wire is surrounded by the gas under investigation, to which it loses heat. Any change in the thermal conductivity of the gas causes a change in the rate of heat loss from the wire and, consequently, in its temperature. Changes in temperature of the wire effect commensurate changes in its resistance which can be measured by means of a sensitive galvanometer. The sensitivity of the apparatus was such that a deflection on the galvanometer scale of 10 cms represented an assimilation rate of 1.44 cm^3 CO_2/hour.

Leaves were placed in a glass assimilation chamber kept at constant temperature in a water bath and illuminated either by a 500 watt incandescent lamp or, in a few experiments, by a high pressure mercury vapour lamp (Type, Philips H.O. 2000). A gas flow of constant velocity passed over the leaf and through the diaferometer, where its heat conductivity was measured against that of gas from the same source, but which had by-passed the leaf and, thus, had not changed in CO_2 content. The gas mixture used was air containing 4.65 % CO_2 and was saturated with water before passing the leaf. The light intensity was varied by interposing combinations of Schott neutral glass filters between the lamp and the assimilation chamber and was measured by means of a selenium barrier-layer photocell held flush to the leaf surface. The temperature of the water bath was regulated by a small 20-watt heating coil or by adding ice.

Since these measurements were carried out on detached leaves, it was desirable to find out, at the outset, for how long the normal rate of photosynthesis was maintained, before the effects of removal from the plant were felt in the leaf. Starting 15 minutes after detaching leaves of *Acer saccharinum* from first year seedlings, measurements of CO_2 assimilation at a light intensity of 20 000 lux and a temperature of 24° C were made for periods of 6 hours continuously. The results of 4 such determinations are shown in Fig. 1. Carbon dioxide uptake has been expressed per unit area per unit time and plotted against time.

The figure demonstrates that for the first three quarters of an hour there is an apparent increase in photosynthesis rate, followed by a steady decline for the next five hours.

For all experiments, therefore, leaves were placed in the assimilation chamber immediately after having been detached from the plant and measurements were started after 45 minutes. All experiments were completed within 2 hours of detaching the leaves. Thus, changes in photosynthetic rate over the period of the experiment and due to uncontrollable factors were probably not great. Measurements of the light intensity dependence of photosynthesis were made at about 24° C; they began with the lowest intensity and worked upwards to the highest. Thus, measurements at the highest light intensities were made when the leaves had been detached from the plant between $1^1/_2$ and 2 hours. In view of the decline in photosynthesis rate with time, it follows that such measurements when compared with those at lower light intensities, are too low. The error introduced, however, was not regarded as serious.

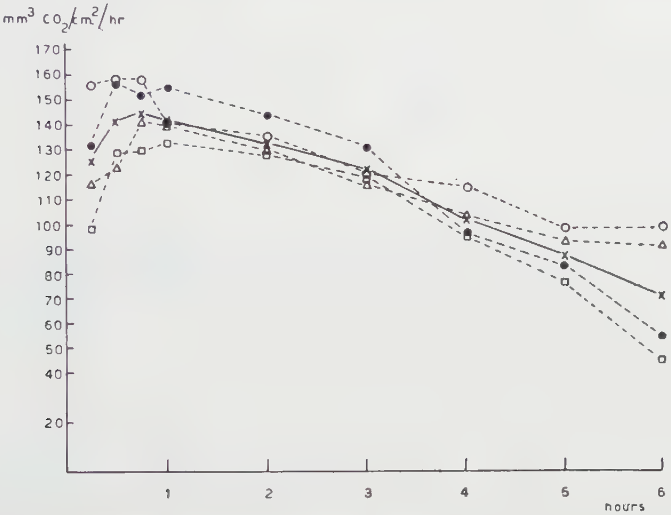

Fig. 1. *Acer saccharinum*. Uptake of carbon dioxide (mm³ CO_2/cm²/hr) by excised leaves plotted against time after detachment from first-year seedlings. The solid line represents the mean of 4 leaves shown by dotted lines.

In all experiments, CO_2 output in the dark was taken as a measure of respiration and it was assumed that light has no influence on respiration. That this is a correct assumption has been questioned by several workers; indeed, according to JAMES (1953), "possible interactions with respiration have been the bugbear of photosynthetic measurements since their beginning". Among others, FOCKLER (1938), MCALISTER and MYERS (1940), and MYERS and BURR (1940) have demonstrated an apparent increase in respiration as a consequence of illumination. KOK (1950), on the basis of experiments at low light intensities, concluded that light reduces or even totally suppresses respiration. On the other hand, recent work with labelled oxygen (O^{18}) has failed to demonstrate any marked effect of light on oxygen uptake by higher plants including several tree species (1951). In the absence of a method of measuring O_2 exchange, therefore, the above assumption was made. Since the output of CO_2 due to respiration relative to the uptake due to photosynthesis is generally very small, serious errors were probably not introduced. Measurements of dark respiration were made immediately before and after the photosynthesis measurements.

Experimental Results

1. *The effect of physiological age of leaf on photosynthesis*

In Figs. 2—6, graphs of CO_2 assimilation against light intensity, for leaves of different physiological ages, have been plotted. Each point represents the mean of 4 determinations. The data from which these figures were obtained are summarised in Table I. The saturation and compensation light intensities were read from the completed figures.

Photosynthesis has been expressed as mm^3 CO_2 assimilated per cm^2 leaf area per hour, for each of the leaf ages used. Leaf areas were determined by tracing on to squared paper at the end of each measurement.

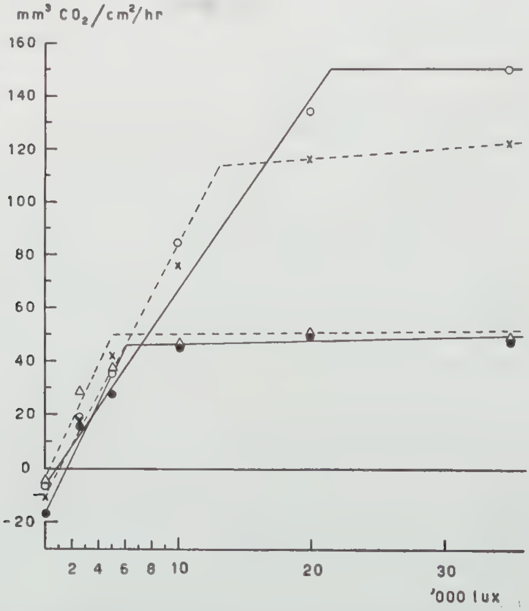

Fig. 2. *Acer pseudoplatanus.* The effect of leaf development stage on the rate of photosynthesis. ●——● young leaf, ×----× half-expanded leaf, ○——○ fully expanded leaf, △----△ old leaf. Each point average of 4 leaves.

TABLE I

Photosynthesis data for detached leaves of different physiological age; means of 4 determinations

Species	Physiological age	Maximum recorded CO_2 uptake ($mm^3/cm^2/hr$)	Mean dark respiration ($mm^3/cm^2/hr$)	Saturation intensity (lux)	Compensation point (lux)	Expt. temperature °C.
Acer pseudoplatanus	Young	50.4	17.36	5950	1618	25.4
	Half-expanded	122.4	10.41	14438	1178	25.4
	Fully-expanded	150.6	6.55	21719	893	25.6
	Old	51.5	4.96	5050	485	25.4
Acer platanoides	Young	18.4	11.70	4888	2300	25.1
	Half-expanded	96.1	5.34	10262	583	25.5
	Fully-expanded	116.3	8.26	19675	1300	25.6
	Old	49.2	4.84	6975	765	25.9
Acer saccharinum	Young	48.0	8.62	3988	653	25.1
	Half-expanded	99.1	6.20	13050	845	25.4
	Fully-expanded	138.0	6.86	21100	1025	25.8
	Old	53.2	5.81	5100	565	25.5
Quercus robur	Young	66.4	6.94	7850	838	25.0
	Half-expanded	94.5	5.42	11763	643	25.6
	Fully-expanded	116.2	3.67	13462	450	25.4
	Old	70.4	4.17	7550	476	25.4
Quercus borealis	Young	56.5	15.72	6700	1518	25.3
	Half-expanded	41.0	6.98	5438	738	25.6
	Fully-expanded	73.3	7.33	12750	1033	25.6
	Old	23.2	3.98	7313	803	25.3

The physiological ages are described as "young", "half-expanded", "fully-expanded" and "old". "Young" leaves are leaves just formed and growing rapidly. They were light green in colour or, in the case

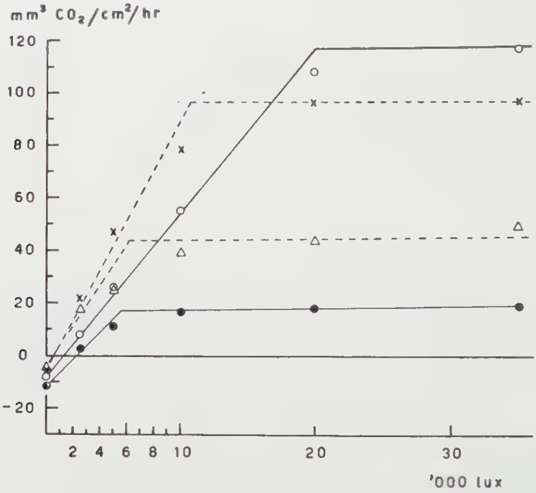

Fig. 3. *Acer platanoides*. The effect of leaf development stage on the rate o photosynthesis. ●———● young leaf, ×– – – –× half-expanded leaf, ○———○ fully expanded leaf, △– – – –△ old leaf. Each point average of 4 leaves.

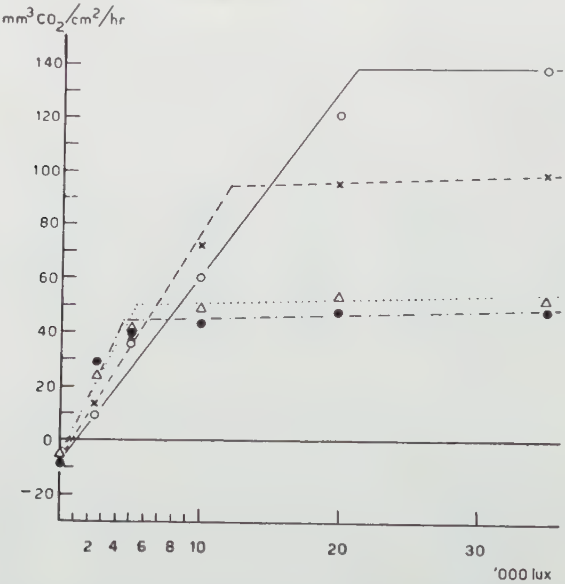

Fig. 4. *Acer saccharinum*. The effect of leaf development stage on the rate of photosynthesis. ●— ——● young leaf, ×– – · – × half-expanded leaf, ○———○ fully expanded leaf, △– – – –△ old leaf. Each point average of 4 leaves.

of *Acer*, were sometimes pale yellow. "Fully-expanded" refers to the youngest fully-expanded leaf on the plant, while "half-expanded" is intermediate between young and fully-expanded. By "old" is meant the oldest fully-expanded leaf present. The actual ages (approximate values only) were as follows:

Species	Young leaves (days)	Half-expanded leaves (days)	Fully-expanded leaves (days)	Old leaves (days)
Acer spp. and *Quercus robur*	4–6	9–12	14–18	35–50
Quercus borealis	2–3	5– 6	10–17	ca. 60

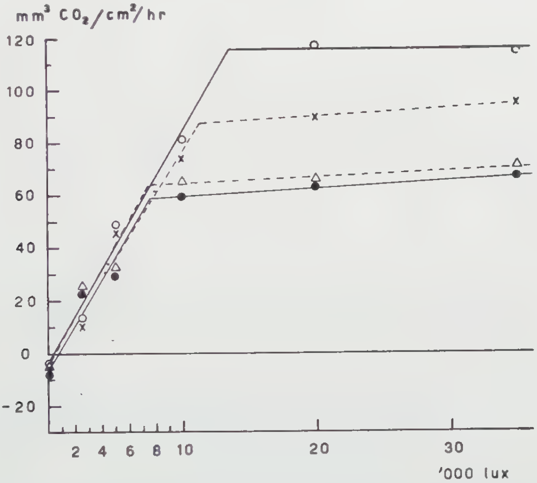

Fig. 5. *Quercus robur.* The effect of leaf development stage on the rate of photosynthesis. ●——● young leaf, ×----× half-expanded leaf, ○——○ fully expanded leaf, △----△ old leaf. Each point average of 4 leaves.

It will be noted that, in the figures, the pre- and post-light-saturation parts of the curves have been prolonged to meet at a point, while in many cases a smooth curve would better fit the plotted values. This has been done in order to obtain a more objective value for the saturation intensity than would otherwise be possible.

It can be seen from the figures and table that, in the case of the *Acer* spp., the maximum level of CO_2 assimilation in very young leaves is relatively low; it is somewhat higher in half-expanded leaves; and highest when the leaves are fully-expanded; the rate in old leaves is about $^1/_2$ to $^1/_3$ of that in fully-expanded leaves. Similarly, the light saturation intensity increases up to full expansion, and then falls when the leaves become old. The compensation point values, however, show no definite trend.

In *Quercus robur* (Fig. 5), the pattern is similar but the maximum levels of photosynthesis and saturation intensities are markedly lower than for any of the *Acer* spp. For *Quercus borealis* (Fig. 6), however, the maximum assimilation level is higher in young than in half-expanded leaves though, again, it is highest in fully-expanded leaves and falls off during senescence. Differences in saturation intensity are less marked and there is little difference between young, half-expanded and old leaves. The highest saturation intensity, however, is again found in fully-expanded leaves.

With regard to absolute values, it is clear that, under the conditions of these experiments, maximum CO_2 assimilation per unit leaf area is relatively greater in the case of *Acer* than in that of *Quercus*.

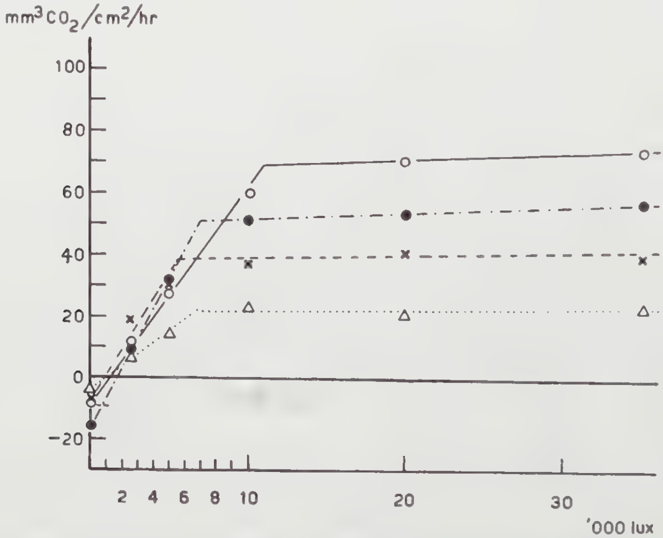

Fig. 6. *Quercus borealis*. The effect of leaf development stage on the rate of photosynthesis. ●———● young leaf, ×----× half-expanded leaf, ○———○ fully expanded leaf, △----△ old leaf. Each point average of 4 leaves.

The values for respiration show the same trends for all species, young leaves showing the highest rate and old leaves the lowest. There is little difference between half-expanded and fully-expanded leaves, and little difference in absolute values between species at these leaf ages. With young leaves, however, the rates of CO_2 output by *Quercus borealis* and *Acer pseudoplatanus* are almost double that of the other species.

2. *The effect of actual age of leaf on photosynthesis*

Having found big differences in CO_2 assimilation between leaves of different physiological age, it seemed of interest to see whether differences in *actual* age have any marked effect. As has already been said, seedlings of *Acer saccharinum* which had grown under extremes of daylength were used. Plants of the types used are illustrated in Fig. 7. The leaf pair numbered 2 in the S.D. plant has been present for the same length of time as that on the LD plant. Due to the more rapid growth of the latter, however, there is a big difference in physiological age between the two leaf pairs; whereas in the short day the 2nd leaf pair is only just fully expanded, in the long day, the corresponding leaf pair is approaching physiological old age. In physiological age,

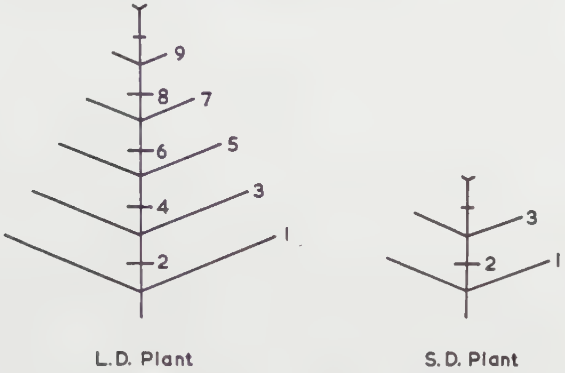

Fig. 7. *Acer saccharinum.* Diagramatic representation of seedlings grown under extremes of daylength. L.D. = 24 hours light per day; S.D. = 10 hours light per day.

the 2nd leaf pair of the S.D. plant compares with the 7th leaf pair of the L.D. seedling.

By measuring CO_2 assimilation in leaves from the 2nd (L.D. and S.D.) and the 7th (L.D.) leaf pairs, therefore, it should be possible to see how differences in actual age compare with differences in physiological age.

The results of such a comparison are given in Fig. 8. Each point in Fig. 8 is the mean of 5 measurements. The close resemblance between the curves for the 2nd S.D. leaf and that for the 7th L.D. pair, together with the entirely different curve for the 2nd L.D. leaf, demonstrates that the relation between maximum assimilation level and physiological age does not extend to actual leaf age.

Discussion

The increase in the rate of photosynthesis during the first 15 minutes n the experiments illustrated in fig. 1 is unlikely to be due to induction phenomena of the kind described by Van der Veen (1949), though Briggs (1933) has shown that induction phases may be of relatively long duration. It may well be due to changes in the rate of gas exchange between the leaf and the surrounding air as a result of an increase in the number of stomata open or in their width. Perhaps an increase in leaf temperature due to illumination is a contributory factor, though this, again, would not be expected to go on for so long.

In general, in these data maximum assimilation level and saturation intensity increase with physiological age up to full leaf expansion as expected. In *Quercus borealis*, however, the maximum assimilation level was higher in young than in half-expanded leaves. There can be little doubt that the observed effect is a real one. An explanation may lie in the relation between internal factors in photosynthesis and leaf expansion. In addition to its dependence upon chlorophyll concentration (which increases steadily with leaf age), the rate of photosynthesis may be determined by other internal factors (e.g. leaf protein) and the absolute amount of such factors may well increase as the leaf grows older. Leaf expansion in *Quercus borealis* is extremely rapid; only 4 days separate "young" and "half-expanded" leaves. Leaf expansion therefore, may outstrip the formation of internal factors, so that, when expressed per unit leaf area, these factors initially decrease with leaf age. Thus, if they limit photosynthesis, this process will show an initial decrease on a leaf area basis. Changes in the level of a single "internal factor" may account for all observed changes in the maximum assimilation rate per unit leaf area. Although the initial rise in rate may be due to an increase in the concentration of chlorophyll with age, the drop in the assimilation rate during leaf senescence cannot be linked with changes in chlorophyll concentration since the latter is reported to increase with age (Stalfelt, 1924; Rabinowitch, 1952). In our material, also,

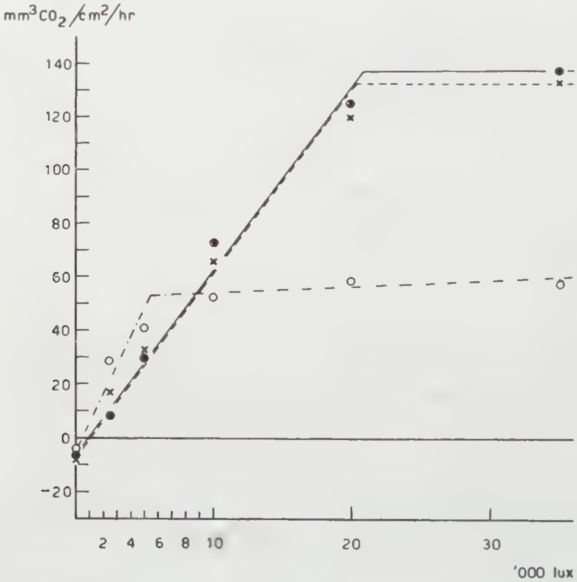

Fig. 8. *Acer saccharinum.* Rate of photosynthesis at ± 25° C. plotted against light intensity for leaves of the same actual age but of different physiological ages (cf. ●———● = 2nd leaf from S.D. plant; and ○·—·—·○ = 2nd leaf from L.D. plant) and for leaves of the same physiological age but of different actual ages (cf. ●———● = 2nd leaf from S.D. plant; and ×----× = 7th leaf from L.D. plant). Each point represents the mean of 4 determinations.

there was no decrease in chlorophyll concentration with age as judged by eye.

In addition to the work of Willstätter and Stoll (1918) and Briggs (1920), most more recent schematic representations of photosynthesis contain several enzyme systems (see Rabinowitch, 1952; Warburg, 1919; Wassink *et al.*, 1938) Moreover, the reduction of CO_2 and the development of O_2 involve a number of enzymatic reactions (Franck and Loomis, 1949). There is some evidence that protein metabolism is intimately bound up with photosynthesis and that the rate of protein synthesis can limit photosynthesis (Burstrom, 1945; Smith, 1944).

It is thus clear that the changes in the maximum level of CO_2 assimilation per unit leaf area reported here need not to be ascribed to any single factor. During leaf expansion possible factors limiting photosynthesis are: chlorophyll concentration, moisture content, or the capacity of any enzyme systems involved. During senescence the limiting factor is almost certainly not chlorophyll but it may be either moisture content or an enzyme.

The assumption that CO_2 output during darkness is an accurate measure of respiration during illumination, may not be correct. Also, the experimental technique was not sufficiently exact for precise measurements on this point. With the galvanometer sensitivity used for these measurements, a deflection of 1 cm. represented a CO_2 output of 144 mm^3/hr. Leaves of about 25 cm^2 area were used, and most of the measurements of CO_2 output are based on scale deflections of less than 15 mm. Since it was possible to read only to the nearest 1 mm, the absolute values are subject to relatively large errors. In all species, the highest rates were shown by the youngest leaves and the lowest rates by the oldest leaves. This confirms the general information that in young leaves the rate of respiration is normally higher than in old leaves, due to the greater proportion of protoplasm in meristematic tissues.

It is of interest to compare the absolute levels of CO_2 assimilation, with those found by other workers. Few measurements of photo-

Species	Maximum rate of photosynthesis (mm^3CO_2/cm^2 leaf surface/hour) ¹)
Aesculus hippocastanum	178.8
Acer Negundo	216.8
Sambucus nigra	184.2
Acer pseudoplatanus ("young leaves")	86,7
Acer pseudoplatanus ("old leaves")	140.9
Tilia cordata ("young leaves")	97.5
Tilia cordata ("old leaves")	151.7
Quercus robur	222.2

¹) Willstätter and Stoll actually present their results as mg CO_2 absorbed /100 cm^2 leaf surface/hr. Their results have been recalculated here as mm^3 $CO_2/cm^2/hr$, so as to make them directly comparable with our data.

synthesis in woody species have been made, and even these lack standardisation in methods of measurement or expression of results. The most extensive data for trees measured under laboratory conditions are those given by WILLSTÄTTER and STOLL (1918). In detached leaves in air enriched with 5 % CO_2 at 20° C, they obtained the following maximum rates of photosynthesis (light and CO_2 saturated. [1])

In an atmosphere containing 6.46 % CO_2 and at a temperature of 21° C, the present author (1952) found maxima in the region of 120.0 for both *Acer pseudoplatanus* and *Quercus robur*.

The data given in Table I show that the maximum assimilation values measured for detached leaves of *Acer saccharinum* (ca. 138.0 for fully-expanded leaves) and *Acer pseudoplatanus* (150.6) are of the same order as those found by Willstätter and Stoll for old leaves of *Acer pseudoplatanus*, but are somewhat higher than those recorded earlier (RICHARDSON, 1952) for the latter species. The *Quercus robur* and *Quercus borealis* figures (mean maximum = 116.2 and 73.3 for fully-expanded leaves) are markedly lower than those found previously for *Quercus borealis* (RICHARDSON, 1952) and very much lower than those recorded by Willstätter and Stoll for *Quercus robur*. The maxima recorded here for leaves of *Quercus borealis* are some 40 % lower than those found in 1951 (RICHARDSON, 1951). However, the seedlings used in 1951 had been grown under field conditions and were, presumably, adapted to the much higher light intensities than those in the present experiments. Photosynthetic adaptation of this kind has been found by previous workers (BOYSEN-JENSEN and MUTTER (1929), GESSNER (1937), BECK (1938), BOHNING (1949) and also in our laboratory WASSINK *et al.* (1956).

On present evidence the conclusion is probably justified that variations in the maximum assimilation level are at the specific rather than the generic level. Cultural conditions (especially light intensity) have a marked influence on the photosynthetic capacity of leaves.

SUMMARY

Determinations of CO_2 assimilation per unit leaf area in relation to light intensity were made with detached leaves of various physiological ages of the following species: *Acer pseudoplatanus* L., *A. platanoides* L., *A. saccharinum* L., *Quercus robur* L., and *Q. borealis maxima* (MARSH) ASHE. Measurements were made using the diaferometer technique, at a temperature of 25° C. and on first year material only.

In general, maximum assimilation level and saturation light intensity increased with physiological age of plant material up to full leaf expansion and then fell off during senescence. In *Quercus borealis*, however, the maximum assimilation level was higher in young than in half-expanded leaves; it was concluded that, in this species, leaf expansion outstrips the rate of formation of an internal factor limiting photosynthesis, thus giving rise to an initial decrease in photosynthesis when expressed per unit leaf area.

An experiment using seedlings of *Acer saccharinum* grown under different daylength conditions and, consequently, in different stages of development, demonstrated

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[1] See table bottom p. 455.

that physiological age is more important than actual age in determining the rate of photosynthesis.

In general, the maximum recorded rates of assimilation were markedly higher in species of *Acer* than in the *Quercus* species. From a comparison of these results with those of previous workers it was concluded that variation in photosynthesis potential are at the specific rather than the generic level and are determined to a great extent by the cultural conditions, especially light intensity.

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CELLULOSE MICELLES IN DEVELOPING FIBERS OF ASPARAGUS

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(*received April 12th, 1957*)

The voluminous literature on cellulosic structure in walls of mature plant cells reflects the intense research interest in that structure. Nevertheless, relatively few investigations have been concerned with the changes which occur in the size and organization of the cellulose micelles (*i.e.*, crystallites) during ontogeny of the cell. The principal object of developmental studies of micellar structure has been the epidermal hair of the cotton seed (CLARK *et al.*, 1930; HESS *et al.*, 1936; SISSON, 1937, 1938; WERGIN, 1937). HEYN (1933, 1934) has contributed an analysis of the X-ray diagram of the walls of young epidermal cells of the *Avena* coleoptile at a single stage of growth, and polarization-optical studies of the parenchyma cells of the same organ have been made by BONNER (1935), PRESTON (1938), and SÖDING (1934). PRESTON and WARDROP (1949) and WARDROP (1949) have studied micellar size, structure, and arrangement in the cambium of conifers.

Many other polarization-optical accounts have dealt only with micellar orientation in growing cell walls (MAAS GEESTERANUS, 1941; GREEN and CHAPMAN, 1955; MAJUMDAR and PRESTON, 1941; MEEUSE, 1938; RITTER and STILLWELL, 1934; ROELOFSEN, 1951a; ROELOFSEN and HOUWINK, 1953; etc.). Numerous electron microscopic studies also consider the problem of orientation, in this case, of the "visible" microfibrils. However, these investigations indicate little of the changes in size of the micelles, their relationship to other wall constituents, or their relative degree of crystallinity. The assumption, that crystalline micelles are being studied rather than single molecules of cellulose, is implicit in the majority of the works mentioned above.

The present account deals with development of the so-called "pericyclic" (Fischer, 1900) fibers in growing shoots of *Asparagus officinalis* L. The cell walls of the fibers are investigated from the standpoints of cellulose structure, degree of crystallinity of the cellulose, micellar size, and micellar orientation. Essentially this study is a roentgenographic account, which has been supplemented by the findings of polarization microscopy. Asparagus has been chosen because of the comparative ease of isolation of its relatively homogeneous fiber region, at the inner border of the cortical parenchyma. The histological development of this fiber tissue plays an important rôle in the assessment of quality of the asparagus shoot as a vegetable.

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[1] This study has been performed in the Laboratories of Physics and Technical Biology of the Technical University in Delft, Holland. The author takes great pleasure in thanking the staffs of these laboratories for their friendly and effective help. The financial aid of the USEF/Netherlands has been deeply appreciated.

MATERIALS AND METHODS

Materials

Emerging "spears" of asparagus shoots were collected in the late spring of 1956 and selected for comparable size and vigor of growth. From each shoot, segments 1 cm. long, 3 mm. wide (tangentially), and 2 mm. thick (radially) were taken at the following distances from the tip: 3–4, 5–6, 8–9, 11–12, and 15–16 cm. Since tissue development proceeds acropetally, these different segments were taken to represent, from apex to base, successively older stages in growth. Elongation was usually just becoming noticeable at the 3–4 cm. level and ending at the level of 11–12 cm. Secondary thickening of the fiber wall, with occasional lignification, was characteristic of the 15–16 cm. level. The segments were preserved in a mixture of formalin, acetic acid, and ethanol according to Johansen (1940).

In order to isolate the fiber region from the cortical parenchyma, on the outer side, and from the "medullary" parenchyma and vascular bundles on the inner side, the segments were first embedded in paraffin by an ethanol-normal butanol-xylol schedule. Cross sections of each segment established the distance of the fiber tissue from the outside (about 180–200 μ) and the radial thickness of the fiber tissue (about 60–75 μ). Preliminary orientation of the segment took place before cutting on a sliding microtome, and a final orientation was made during the first contact cuts. Successive 10 μ tangential sections were made, until reaching just into the fiber zone (about 10 μ into its outer edge). This latter was then isolated as a "fiber segment" slab by a single cut which was 10 μ thinner than the measured thickness of the fiber region.

Because of the cylindrical shape of the shoot, it was possible that curvature of the stem might bring other tissues into the edge of the fiber segment. Therefore, after being cut, the slab was placed in a xylol-filled Petri dish on the stage of a dissecting microscope. Foreign tissue was excised with a spear-pointed needle. Upon several washings in fresh xylol, the segments were ready for use.

X-ray observations

For the different roentgenographic methods it was necessary to vary the conditions of observation somewhat. To obtain X-ray diagrams of the unaltered fibers, tissue segments were superposed, successively, on a specimen holder-tangential faces in contact and longitudinal axes parallel. They were held together by Canada balsam, applied in a dilute solution of xylol. These were then placed in the path of an X-ray beam, Cu-Ka, filtered by a nickel foil, 10 μ thick. The collimator diameter was 0.5 mm., in lead glass, and the beam was intercepted by Ilford X-ray film in a flat cassette 40 mm. from the specimen.

In order to obtain X-ray diffraction patterns due primarily to the cellulose of the fibers, the xylol-washed segments were brought into water through the agency of ethanol. They were then extracted of non-cellulosic materials in solutions of 0.2 N HCl and 0.2 N NaOH, successively, for 2 hours in each solution at 97° C. in a water bath. Because of the great decrease in rigidity of the segments (Frey-Wyssling, 1952, gives the cellulose content of young cell walls as 2.5 %), it was not possible to mount more than three segments in uniform orientation on the perforated specimen holder. After drying, the segments were exposed to the same X-ray conditions as above, but in a vacuum camera, with the flat film 30 mm. from the specimen. This arrangement served to minimize the amount of X-radiation scattered by air for the very thin samples and also decreased the exposure time.

Crystallinity percentage was determined on other, similarly extracted tissue segments which were packed in random orientation in a small rodlet according to the method of Hermans and Weidinger (1948). However, the sample shape was changed slightly to that of a right cylinder, 1.6 mm. in diameter, after Wijnman (1954). The films were photometered with a 5 × translation of the traverse course. The calculated crystalline and amorphous indexes were converted to percent crystallinity by fitting to a crystallinity "nomogram" (Hermans and Weidinger, 1949) [1].

With a smaller sample of the Wijnman type (rod of 0.8 mm. diameter), in which the purified fibers were again packed in random orientation, half-breadth determinations were made for the estimation of micellar size of the cellulose. Exposure of the sample to the X-ray beam took place in a cylindrical (Debye-Scherrer type) camera, b7.3 mm. in diameter. The collimator, which must be small relative to the size of the sample, had an aperture diameter of 0.25 mm.

Because the collimator was 5 cm. long, the divergence of the beam at the end of the collimator was greatly minimized. Therefore the assumptions and equations of Hengstenberg and Mark (1929) were inapplicable. The procedure of calculation was as follows (Lonsdale, 1948): considering that the part of line broadening due to particle size is given by $\beta = \sqrt{B^2 - b^2}$ (where b is the line width, in radians, for particles larger than 1 μ in size and B is the measured line width, in radians, at half the height of the photometered peak above the background), then $t = \frac{C\lambda}{\beta} \sec \theta$. (C is a constant, λ the wavelength of the X-radiation, θ the reflection angle or Bragg angle, and t the diameter of uniform spherical particles with cubic symmetry.) In the present case, b was determined by making a mixture of coarsely-crystalline NaCl and purified cotton fiber in the form of a rodlet, 0.8 mm. in diameter. Thus, b values were established under the same conditions as B, and b for the desired cellulosic interference was obtained by interpolation.

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[1] The author is greatly indebted to Dr. A. Weidinger for his help with the equipment and calculations in this method.

The least equivocal interference for line breadth determinations in the powder diagram was that of the (002) plane, which gave the micelle diameter perpendicular to that plane. Overlapping of the (021) interference could be corrected easily by establishing the slope of the (002) peak. This was not possible in the overlapping of the (101) and ($10\bar{1}$) interferences. Half-breadth values were corrected for the slope of the background line according to the equation given by Frey-Wyssling (1937). Micelle length is impossible to ascertain in a powder diagram because of the coincidence of 4–10 interferences with the (040) peak [*e.g.*, equatorial ($20\bar{2}$), (301), ($30\bar{1}$), (103) and very likely also (310), (230), (221), ($22\bar{1}$), (130), and (131)].

Polarization observations

For control of observations on micellar orientation, polarized light was employed. For this purpose, 2 μ–5 μ sections were cut transversely and in radial-longitudinal planes from shoot segments embedded in paraffin blocks. After removal of the paraffin, these were either mounted in Canada balsam unstained or stained with Congo red or benzoazurin before mounting. In addition, fiber tissue segments were brought to an aqueous medium (as described above) and then macerated by warming gently in a mixture of 1 % chromic acid–8 % nitric acid, followed by shaking. After washing, the separated fiber cells could be mounted, stained or unstained, in Canada balsam for study. Occasionally the cells were crushed in order that single cell walls might be observed. To enhance sensitivity, a strong white light source was used, and the slow axis of the Red I plate was placed near the plane of the polarizer in the NE-SW quadrants (Laves and Ernst, 1943).

Results

Crystalline pattern

There is a notable pattern change of crystalline interferences in the untreated fiber tissue as a function of age, as is indicated in Fig. 1–3. These figures show an increase in intensity of the outermost of three rings [at 3.96 – 4.02 Å, perhaps representing the (002) and (021) planes of cellulose], the widening of the middle ring [which has the position of the ($10\bar{1}$) plane of cellulose] to include the spacing which would be the (101) plane of cellulose as a new ring, an intensity increase in the middle ring, and the gradual decrease of intensity of the innermost broad ring, which represents spacings of 9.6 to 15.5 Å. In the original negatives, there is also a gradual decrease of intensity of a weak ring at 2.36 Å, coincident with an increase in intensity of a ring at 2.56–2.63 Å [the latter representing the interferences in the neighborhood of cellulosic (040)].

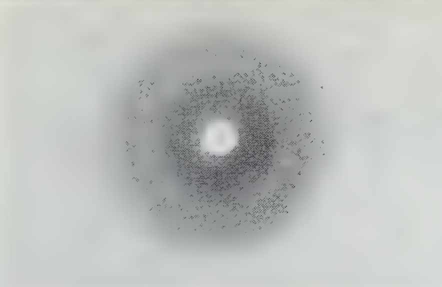

Fig. 1. At 3–4 cm level in shoot (start of elongation)

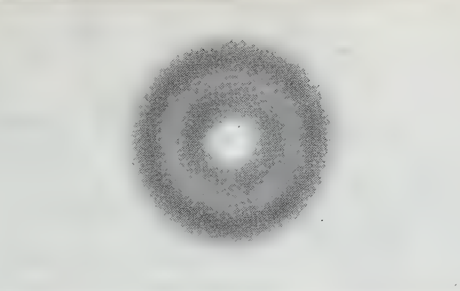

Fig. 2. At 11–12 cm level in shoot (maximum elongation)

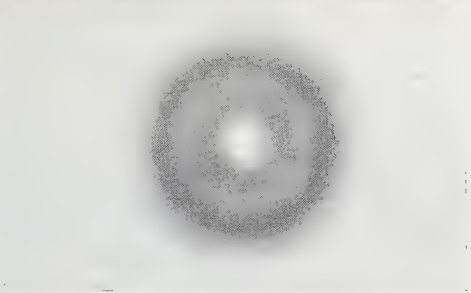

Fig. 3. At 15.16 cm level in shoot (start of secondary wall thickening)

Fig. 1–3. X-ray diffraction patterns of untreated asparagus fiber tissue. Fiber axis vertical. Specimen-to-film distance is 40 mm.

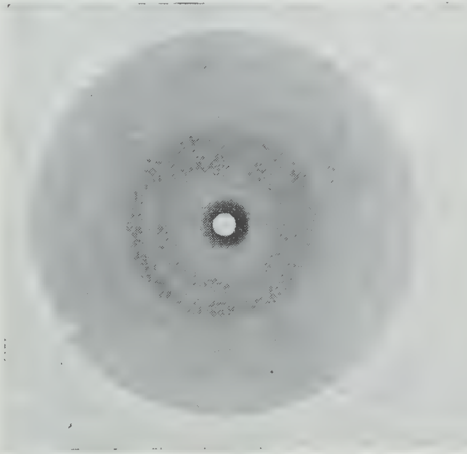

Fig. 4. At 3–4 cm level in shoot.

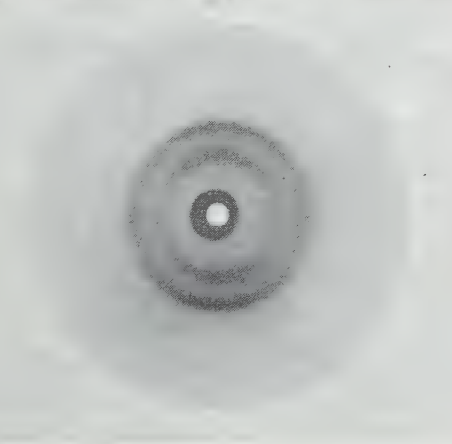

Fig. 5. At 11–12 cm level in shoot.

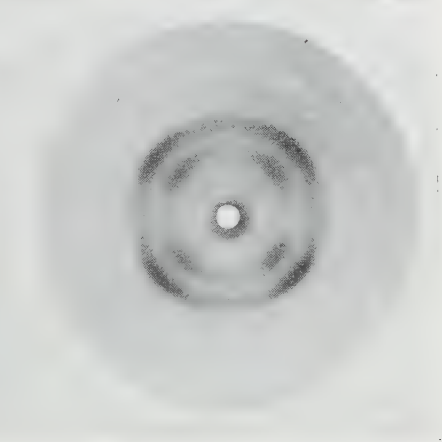

Fig. 6. At 15.16 cm level in shoot.

Fig. 4-6. X-ray diffraction patterns of asparagus fiber tissue after extraction of non-cellulosic material. Fiber axis vertical. Specimen-to-film distance is 30 mm.

Organization of cellulose

After the non-cellulosic constituents have been removed from the fiber segments, the cellulosic interferences are visible at all stages of development. Fig. 4–6 indicate that the main crystalline spacings of the cellulose lattice are present at all significant stages: youngest, greatest elongation, and beginning of secondary wall thickening. It may also be seen that the orientation of the cellulose micelles is more or less at random at the 3–4 cm. level (continuous rings), mainly lying in horizontal orientation at 11–12 cm. [the (002) and (101)-(10$\bar{1}$) spacings have a transverse position in Fig. 5], and indicative of a crossed fibrillar arrangement at 15–16 cm. (Fig. 6). In this last figure, the micelles are almost at right angles to each other: the inclination of the micellar long axis to the long axis of the cell is about 48–51°. It is also to be noted that, as in the untreated fibers, there is a progressive differentiation of the diffraction rings. In particular, the (021) spacing becomes quite distinct from that of (002) in the diagram of the 15–16 cm. fibers, both by radial and angular separation.

Degree of crystallinity

A typical comparison photometric recording is given in Fig. 7. The cellulosic diagram is at the right and the comparison substance at the left. The amorphous background is indicated by the dashed line; the air scatter effect by the dotted line. The relative surface area of the curve of cellulosic peaks above the amorphous background is determined for each sample. This value, divided by the peak height of the photometric curve for the comparison substance, gives the

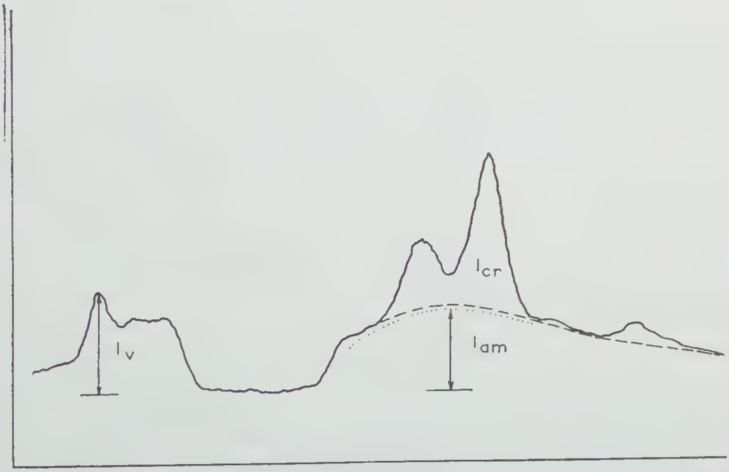

Fig. 7. Photometric traverse of X-ray diffraction pattern of an extracted fiber specimen (at right) and comparison material (at left). This is from the 15–16 cm level. I_{cr} is the crystalline surface area; I_{am} is the maximum height of the amorphous background after correcting for air-scatter; and I_v is the height of the peak of the comparison material.

crystalline index for the sample. The relative height of the amorphous portion of the cellulose curve represents the amorphous index of the sample. Both values establish a point for each sample, and these points have been plotted on the crystallinity nomogram in Fig. 8. The nomogram is determined on the basis of well-defined "crystallinity" values for native plant fibers with highly crystalline cellulose (*e.g.*, ramie, cotton, and flax) at point B and for more amorphous types of regenerated cellulose, such as rayons and cellophane, at point A. (The crystallinity of native fibers is taken as 70 % and that of rayons as 39 %.)

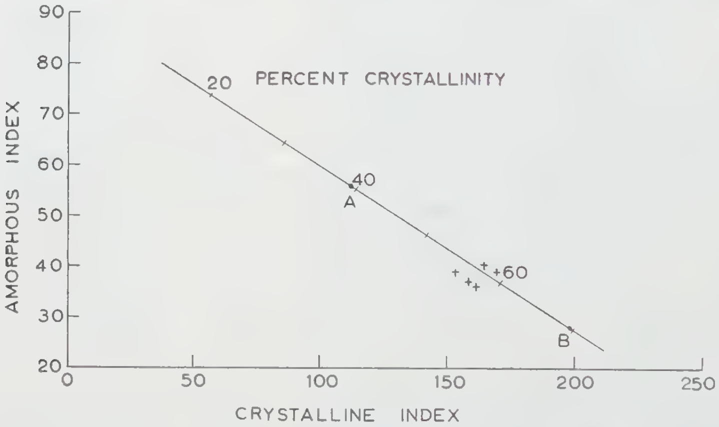

Fig. 8. Crystallinity nomogram. Asparagus specimens are represented by + marks. Points A and B are used to establish the line and the values of percentage of crystallinity. (Further explanation in text.)

When so plotted, the crystallinity values for the various stages of asparagus development fall within a fairly close range. No principal differences are apparent among the samples with respect to the degree of crystallinity, and no developmental trend is indicated. All the values occur between the points of 55 and 60 % crystallinity.

Micellar size

Table I presents the measured half-breadth values and the steps in calculation of the micellar diameter for the (002) interference in the asparagus samples and in similarly purified cotton and ramie fibers. The value for micelle diameter in ramie was 59 Å. It is of interest to note that HENGSTENBERG and MARK (1929) found the micelle diameter in ramie to be 56 ± 5 Å, FREY-WYSSLING (1937), 56 Å, and KRATKY *et al.* (1942), 65 Å, with different X-ray techniques and different methods of calculation from that used here. With ultra-sonic disintegration of fibers of ramie, hemp, cotton, etc., WUHRMANN *et al.* (1946) observed that the smallest strands seen in the electron microscope were also 60–70 Å wide.

The micellar diameter for asparagus fiber cellulose increases slightly during fiber elongation. However, at the end of elongation, the micelle size is not markedly different from that at the initial stages of growth. At the beginning of secondary wall formation, a conspicuous increase in the average micellar diameter is to be seen.

Table I

Half-breadth values of (002) interference and calculations for micelle diameter of cellulose in asparagus fibers

Sample Asparagus fibers	Measured half-breadth on film (mm)	B'* (mm)	B'^2	B'^2-b^2**	β ($\sqrt{B'^2-b^2}$) (mm)	β (radians)	t*** (Å)
3– 4 cm	1.56	1.50	2.25	2.14	1.46	0.051	28
5– 6 cm	1.46	1.43	2.04	1.93	1.39	0.049	29
8– 9 cm	1.40	1.40	1.96	1.85	1.36	0.047	30
11–12 cm	1.40	1.40	1.96	1.85	1.36	0.047	30
15–16 cm	1.10	1.10	1.21	1.10	1.05	0.037	38
Cotton fibers	0.71	0.71	0.50	0.39	0.63	0.022	64
Ramie fibers	0.77	0.77	0.59	0.48	0.69	0.024	59

* B' is a corrected half-breadth value, obtained by multiplying the measured value on the film by a correction factor which depends upon the relative slope of the background (Frey–Wyssling, 1937).

** b^2 is 0.11 for the (002) interference under the experimental conditions used here.

*** t is the micelle diameter, from $t = \frac{C\lambda}{\beta} \sec \theta$, where θ is 11.4°, C is 0.9, and λ is 1.54 Å.

The photometric curves of the purified cellulose of the elongating samples (used in the estimation of micellar diameter) are quite similar to one another and may be represented by the curve for the 3–4 cm. sample (Fig. 9). The (002) peak is relatively low, and there is a poor differentiation of such adjoining interferences as (021)–(002) and (101)–(10$\bar{1}$). At the initiation of secondary wall thickening (Fig. 10), the (002) peak is much higher above both the background and the (021) interference, and the (101) and (10$\bar{1}$) peaks are somewhat more distinctly separated. In cotton (Fig. 11), the (002) peak is quite high and narrow, and (021) is clearly set off from it; the tips of (101) and (10$\bar{1}$) are definitely separate and differ conspicuously in height.

Aspects in polarized light

In surface view, the cells at 3–4 cm. are isotropic, but in longitudinal section, the wall edges have a weak positive birefringence with respect to the long axis of the cell, and in transverse section to its periphery. Negative birefringence is first noticeable in the face view of the 8–9 cm. fibers, *i.e.*, in the surface view of the single cell wall as seen in longitudinal section and of the double cell wall, both in section and in macerated whole cells. At this level, the fibers are already 400–500 μ long.

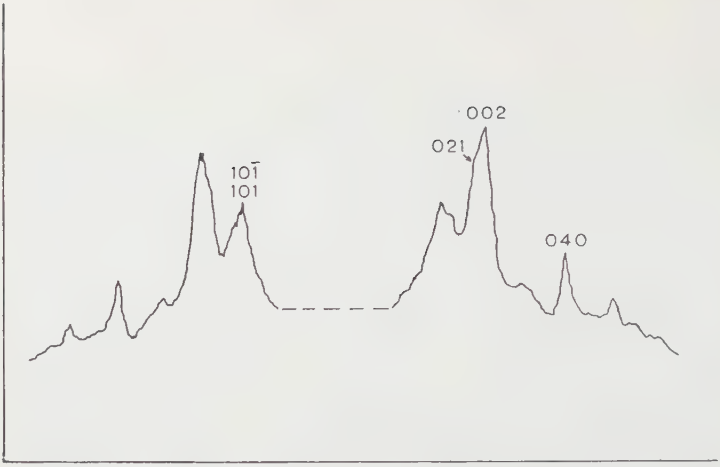

Fig. 9. At 3–4 cm level in asparagus shoot.

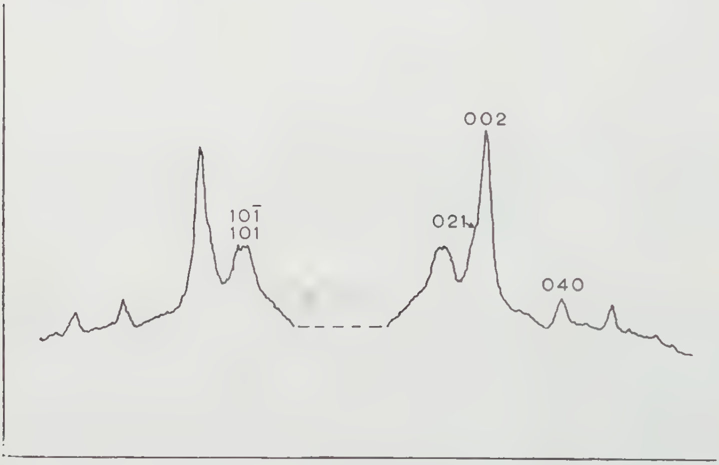

Fig. 10. At 15–16 cm level in asparagus shoot.

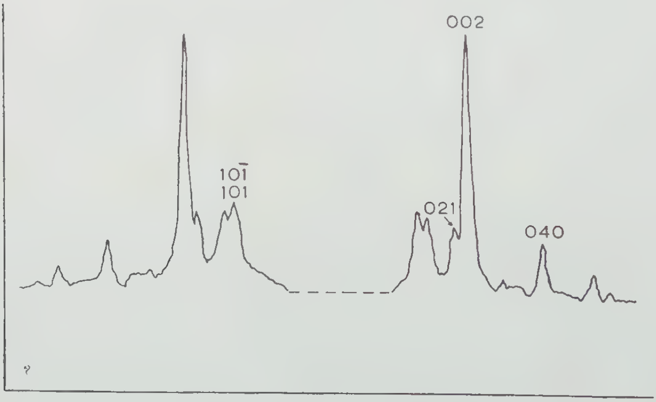

Fig. 11. Cotton fibers.

Fig. 9–11. Photometric traverses of X-ray diffraction pattern of extracted fiber specimens used in determinations of micellar diameters.

At the level of 11–12 cm., the fibers are full-sized, varying in length usually between 700 and 900 μ, hence are almost twice as long as at the 8–9 cm. level. The polarization aspect is much as at 8–9 cm.: in whole cells, both the single and double walls are negatively birefringent in surface views. (The same is true of surface views in section, but the wall edges remain positively birefringent with respect to cell length and cell periphery.) In all cases, the birefringence is relatively weak and needs special techniques for its demonstration, including the benzoazurin staining, strong light source, and altered position of the Red I plate.

At the 15–16 cm. level, the cell wall is considerably thicker and is more strongly birefringent. The double wall is still negatively birefringent with respect to cell length, but single walls have a major extinction position (MEP) at about 45° to the long axis of the cell. When a macerated whole cell is partly stretched, so that some wall tearing occurs with an "unrolling" effect along the line of the MEP, it can readily be seen that the opposite side of the cell has its MEP opposed to the direction of that of the near side.

The opposed directions of the MEP of opposite sides of the cell wall at 15–16 cm. may also be noted without the use of a Red I plate if the cells be stained with safranin. In this case, there is also a blue-yellow color effect. A blue color is achieved when the MEP of the safranin-stained wall lies in the NW-SE quadrants, and a yellow color is produced with the MEP in the NE-SW quadrants. In younger cells and in unstained cells at the 15–16 cm. level, the wall is darkened if the MEP lies in the NE-SW quadrants and is bright if the MEP is in the NW-SE quadrants. These effects appear to be those of crossed-plate relationships, which have been discussed by FREY-WYSSLING (1941), ROELOFSEN (1951), and others.

DISCUSSION

Concerning the broad outlines of micellar orientation in the growing cell wall, this study has corroborated the results of most previous authors. In the youngest stage, the evidence of X-rays and polarized light indicates that the micelles are arranged at random in face view but do tend to have a foliar (uniplanar) texture (Frey-Wyssling, 1930), *i.e.*, at any given depth in the wall, the micelles are arranged in the plane of the wall, perpendicular to a radius from the center of the cell.

During elongation, proportionately more micelles tend to be oriented as well in the transverse direction, to give the so-called "tubular texture" (FREY-WYSSLING, 1930). Apparently, the longer the period of growth goes on, the more predominant becomes the transverse orientation of the micelles. With secondary thickening, the next micelles are laid down in close array in a helix at an angle slightly more than 45° (*ca.* 48–51°) to the vertical axis of the cell. Hence the view through the double wall shows a negative birefringence with respect to cell length.

Various workers have revealed the presence of ambiguous (for cellulose) spacings in the X-ray diffraction diagram of cell walls. These spacings frequently disappear after treatment of the walls for the removal of non-cellulosic components. SEN and WOODS (1949) found spacings of 9.7 and 14.6 Å in jute, SISSON (1938) noted a 14.5 Å equatorial spacing in young cotton hairs, ROELOFSEN et al. (1953) have indicated a spacing of about 13 Å in *Halicystis* (which became intensified after NaOH treatment), and perhaps a similar one may be seen in Fig. 2 of PRESTON's (1951) study on microfibrillar structure in *Valonia*. The present investigation has shown a broad spacing of 9.6–15.5 Å in elongating asparagus fibers. This spacing diminishes greatly in intensity when secondary walls are being deposited, and it disappears completely on treatment of the cells with hot dilute HCl and hot dilute NaOH.

Elsewhere, the author (STERLING, in press) has found a spacing of 12–15 Å as a strong interference in the X-ray diagrams of certain gels of pectic and alginic acids and their calcium salts. He has suggested that this may be a spacing of a polyuronide lattice structure which does not occur in the stretched fibers which are usually made for the study of unit cell construction. Hence, except for the spacing found by ROELOFSEN *et al.* (1953), it is conceivable that the unexplained spacings noted above are those of polyuronide materials. No evidence was found for the "primary substance" rings of HESS *et al.* (1936), which were later considered as those of waxes. However, their ring at 4.2 Å and HEYN's (1933, 1934) of the same size could well correspond to the strong meridional spacing, at 4.2 Å, of pectic materials.

Contrary to the results of CLARK *et al.* (1930) on cotton, the cellulosic interplanar distances of the asparagus fibers do not decrease during growth but remain constant. According to HEYN (1934), the cellulose of the young cell wall is not completely crystalline. Supposedly a regular structure is present at first only in the direction of a spacing $d = 4.18$ Å [(002) + (021) and/or pectin?]. It is of interest that HERMANS (1949) also conceives of differences of degree of "lateral order" (*i.e.*, crystallinity) in the crystallites of the modified cellulose of rayon, so that a 2-dimensional order in its lattice may be envisioned.

Possibly the delayed appearance of the (101) plane in the X-ray diffraction pattern of untreated asparagus indicates the previous existence of an imperfectly crystalline state. (Of course, orientation of the (101) plane parallel to the tangential plane of the segment is possible, but this has not yet been definitely shown for the cell walls of higher plants. Since the segments of untreated fiber tissue scarcely shrank at all during drying in the xylol-balsam solution and were dried down over an opening in the specimen holder, there was no orienting stress due to drying.) PRESTON and WARDROP (1949) also found that the diffraction spacing for the (101) plane was absent in untreated cambial cell walls although present in purified material. If the lattice structure were incomplete, it could contribute to the amorphous index in the HERMANS and WEIDINGER (1948) method of crystallinity determination.

Thus, it may be thought that the removal of non-cellulosic substances from the wall does not reveal a crystalline state which is already present but rather permits the better orientation of imperfectly oriented molecules to a lattice structure (WARDROP, 1949). On treating cellulose fibers with acid, HERMANS and WEIDINGER (1949a) obtained an increase in crystallinity in rayons and no change in the crystallinity of ramie. The rayon result was explained in terms of the cutting of chains in the amorphous regions, thereby permitting freer rotation of entangled chains. However, FOSTER and WARDROP (1951) believe that this effect is achieved simply by the hydrolytic removal of the regions of the lowest lateral order and by the removal of the smallest micelles.

HESS *et al.* (1939) are also of the opinion that the cellulose of the primary wall is not yet arranged in a good lattice structure, hence gives a much vaguer type of X-ray diagram. However, after working with young cotton fibers, SISSON (1937) concluded that the process of purifying the cell wall of non-cellulosic substances does not regenerate, hydrolyze, crystallize, or orient precellulosic or unorganized substances, but that it unmasks the crystalline cellulose already present. He explains the non-detection of cellulosic interferences as being due to the very small amount of cellulose in the primary wall (see also FREY-WYSSLING, 1952) and possibly the manner of combination of the non-cellulosic materials with the cellulose. Similarly, ASTBURY *et al.* (1935) believe that the removal of the hemicelluloses from the cell wall simply takes away a more amorphous component, whose direction, spacings, and lateral order in the cellulosic interstices closely resemble those of cellulose.

Few data are available on the proportion of crystalline cellulose in the cellulosic substance of young cell walls. FREY-WYSSLING (1954) has reported 34 % crystallinity in cells of the root tip of corn (also a monocotyledon, like asparagus) and 37 % in the cells of its coleoptile. However, the youngest fiber cells of asparagus have a crystallinity of *ca.* 57 % following a relatively mild extractive procedure. Possibly Frey-Wyssling's material was not adequately purified of non-cellulosic components. It is of interest that the percentage crystallinity here changes little from the youngest stage of fiber development to the stage of secondary wall deposition. The cellulose of older tracheids of *Pinus radiata* and that of fibers of bamboo—again a monocot—likewise have a degree of crystallinity of 50–60 % (PRESTON *et al.*, 1950), although it has been suggested that there were impurities in some of these materials.

Recently it has been speculated that the microfibril of cellulose is essentially a micelle string, *i.e.*, that the diameter of the microfibril is equivalent to that of the micelle (RÅNBY, 1952; BALASHOV and PRESTON, 1955, in *Valonia*). In the asparagus, micellar diameter at the earliest stage is computed to be 28 Å. This agrees quite closely with the dimension of 26 Å, reported by WARDROP (1949) for extracted primary cell walls of *Pinus* cambium and *Avena* coleoptile parenchyma. However, microfibrils of such small size have not been found in young cell walls. The micellar size increases slowly during cell elongation, as also described by Clark *et al.* (1930) in cotton. The sudden increase in micellar diameter (*i.e.*, sudden narrowing in half-breadth values) with secondary wall deposition indicates a real change in the new micelles being deposited. Whether that change is actually one of increased diameter or more perfect lattice structure cannot be decided on the basis of the evidence at hand.

It must be pointed out here that there is no general agreement on the validity of estimation of a precise micellar diameter from measurement of line-broadening values. The assumptions, which underlie all such estimations, of uniform micellar size, perfect lattice structure, cubic symmetry, theoretical point source of X-ray beam, etc. are not borne out in actuality. The value obtained is a parameter which is related to micellar size and must be interpreted in this relative context.

SUMMARY

An X-ray diffraction and polarization-optical study of the cell wall of developing fibers of the shoot of *Asparagus officinalis* L. has been made. The cellulose micelles are randomly arranged in very young cells but assume a statistically more transverse position during elongation. The micelles of the secondary wall are deposited in a helical angle of about 48–51° to the long axis of the cell.

Although the degree of crystallinity remains constant at 55–60 % during all stages of development, micellar size appears to increase slowly during elongation and markedly during secondary wall formation. The significance of micellar size determinations and crystallinity interpretations is discussed.

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ON THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS ON THE OSMOTIC BEHAVIOUR OF ISOLATED PROTOPLASTS OF ALLIUM CEPA

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Chapter I

Introduction

§ 1. Motive of the present investigation

In 1936 Levitt, Scarth and Gibbs described a micro-cinematographic method by the aid of which they had studied the permeability for water of isolated protoplasts. The latter had been obtained from the scales of onion bulbs. Changes in the osmotic value of the medium were found to be followed by changes in the volume of the protoplasts. Since the latter may be regarded as perfect spheres, their volume is proportional to the third power of the diameter. The changes in diameter were automatically recorded on a photographic film, and they could therefore be measured accurately.

In 1937 this method was adopted at the Botanical Laboratory, Utrecht, where it has since been used to test the hypothesis brought forward by Koningsberger (1942), Veldtra (1944) and Bungenberg de Jong and collaborators (1947–1957) concerning the primary effect of growth substances of the auxin type. These authors supposed that this would be the adsorption of the growth-substance molecules to lipidic phases in the protoplasm, where they would act as "sensitizers" in boundary layers in the sense of Bungenberg de Jong and Saubert (1937), and change the physico-chemical properties of lipidic or lipo-protein membranes in the protoplasm. These hypothetic membranes of submicroscopical dimensions inside the protoplasm are not accessible to experiments, and their presence remains therefore open to doubt.

However, the boundary layer of the ectoplasm, and also that of the tonoplast, are supposed to be membranes of the same type, and these layers are more promising objects for experimental investigation, especially the boundary layer of the ectoplasm. It was therefore tried to find out whether the properties of the latter are affected by growth substances. This should manifest itself in a change in the permeability for water.

The classic method of determining the permeability for water by measuring the rate of deplasmolysis of plasmolysed cells, has one disadvantage, viz. that growth substances, when applied in very low concentrations, may be totally or for a large part adsorbed to the cell wall. Such an adsorption would, of course, obscure the effect of the growth substance on the protoplast itself. For this reason it was decided to work with protoplasts isolated from the cell.

The method of LEVITT et al. has been applied since 1937 at Utrecht by a team of senior students under the direction of V. J. KONINGSBERGER and J. B. THOMAS. Because of the war the work had to be stopped in 1942. A preliminary account of the results has been given by KONINGSBERGER (1947, b).

As reported by Koningsberger, the behaviour of the protoplasts appeared to be far more complicated than could have been expected from a mere osmotic system. According to the season, the pretreatment, and the presence or absence of certain ions in the medium, the behaviour of the individual protoplasts proved to be quite different. Because of this variability it appeared impossible to obtain constant and reproducible results by observations made on single protoplasts, as the investigators up to now had tried to do.

The investigations were resumed in 1948 by C. P. A. Duym and D. Vreugdenhil. They recognized that the method had to be altered in such a way that it would become possible to observe several protoplasts at a time. It further proved indispensable to investigate the behaviour of the protoplasts in relation to common environmental factors, prior to a study of the influence of growth substances on the protoplasm.

The present paper deals with the measures taken to improve the method of experimenting as well as the evaluation of the results, and with the effect of temperature, of the proportion of K- and Ca-ions and of certain other cations on the permeability for water of isolated protoplasts.

The experimental work has been greatly facilitated by the constant assistance of a senior student. I gratefully acknowledge the kind cooperation lent successively by Messrs Th. M. J. Mees, P. J. Romeyn, H. Konings and E. Kliphuis.

§ 2. HISTORICAL SURVEY

Observations on protoplasts outside the cell wall by which they are normally surrounded, have already been reported at an early date. DE GLEICHEN (1799) was the first to describe the phenomenon, but he was as yet unaware of the opportunities it offered for experimental research. In this respect the work of DUJARDIN (1835) was of greater value. De Gleichen described the "exudation" of a "sarcode" out of the cells of *Fasciola hepatica*, and saw that it desintegrated only very slowly in water. In one experiment he noticed that this sarcode, unlike other mucous substances, does not immediately dissolve in the presence of potash, and he concluded from this that it really is "une gelée vivante". His description of the desintegration of these spherical bodies into numerous vesicles reminds one of the "frothy degeneration" of the protoplasm that is caused by osmotic processes (KÜSTER, 1929).

The term "protoplasm" was introduced by PURKINJE (1840) for the contents of animal cells, but independently of the latter Von Mohl (1846) came forward with the same term, but by him it was used for the contents of living cells in general. Since then the older term "sarcode" has been replaced by "protoplast"; De Bary (1862) already stated that "Sarcodestränge jetzt wohl besser Protoplasmastränge zu nennen sind".

The occurrence of free protoplasts in the form of swarm spores has probably been reported for the first time in *Vaucheria* by Vaucher (1803), who regarded the extrication of the protoplasm as the emptying of a male organ. Thuret (1843) and Nägeli (1844) recognized that these swarm spores are free protoplasts, and Pringsheim (1854) came to the same conclusion with regard to the swarm spores of *Achlya*. Nägeli (1844), in his study on cell formation and growth, stated that the protoplasm in the cells of an alga may assume a spherical shape when the latter is immersed in a salt solution, and that this rounding-off does not only occur inside the cell wall, but also when the protoplasm is extruded, as happens when the cells are wounded.

Hofmeister (1867) believed that the protoplasm assumes a spherical shape when external form-determining forces are absent, i.e. when the cell wall is no longer present. He overlooked, however, the fact that the surface of the protoplast, because of the surface tension, tries to assume the smallest possible dimension. Hofmeister further supposed that the protoplasm forms a membrane, when it leaves the cell and that this process is only slightly influenced by mechanical intervention. The cohesion and elasticity of this membrane would be low.

According to Pfeffer (1877) and to De Vries (1877) such a membrane would always be present, also in normal protoplasts inside the cell wall. Both authors recognized that this membrane is "semipermeable", at least so long as the protoplasm is living. It was De Vries who coined the term "plasmolysis" for the phenomenon that the protoplasm contracts and frees itself from the cell wall when the cells are immersed in hypertonic media. He further found by means of "abnormal plasmolysis", which takes place when highly hypertonic media are used, that the vacuole is surrounded by a similar membrane, the "tonoplast". The latter too is a semipermeable membrane. His student Went (1887) endorsed his view that the vacuole as well as the tonoplast are to be regarded as independent cell organs. With regard to the tonoplast this view is based on experiments in which, either by wounding the cells or by abnormal plasmolysis, the vacuoles were freed from the surrounding protoplasm and extruded from the cells.

Since the time of Pfeffer and de Vries much research has been devoted to the problem of the particular kind of permeability exhibited by these protoplasmic membranes, the ectoplasm and the tonoplast.

Up to 1910 observations on protoplasts isolated from the cell wall had been of a more or less incidental nature, but in that year a systematic research on the properties of such protoplasts was begun by Küster, who used a method introduced by Af Klercker (1892).

Small portions of mesophyll taken from the bulb scales of *Allium* were plasmolysed in solutions of $Ca(No_3)_2$, and subsequently torn up under a binocular microscope; alongside the fissure the protoplasts are then extruded. Af Klercker had already emphasized that for several purposes, e.g. for the study of the growth and the elasticity of the protoplasm, isolated protoplasts are more suitable than intact cells. He calculated the ratio between osmotic pressure and volume for isolated protoplasts of *Stratiotes aloides*, and found that the results agreed with the expectation so long as the volume of the protoplasts did not exceed the size of the cells from which they were obtained. This led him to the conclusion that below this limit the "elasticity" is constant. He also pointed out that in injured protoplasts an intact tonoplast may be left.

Küster (1928) made a similar observation, viz. that after the isolation of the protoplasts the preparations may contain, besides intact protoplasts, tonoplasts and globular fragments of protoplasts provided with a nucleus or with portions of the vacuole.

Besides mechanical means for isolating protoplasts enzymatic ones have been used. Giaja (1919) isolated the protoplasts from yeast cells by digesting the cell wall by means of gastric juice obtained from the snail *Helix pomatia*. In the fruits of several plants, e.g. of *Solanum nigrum*, the cell walls are hydrolysed during the ripening process, so that free protoplasts are left. Küster (1910 and 1928) used such protoplasts for studying their capacity to fuse. He preferred this physiological method for isolating protoplasts to the mechanical one, because the latter may easily damage the protoplasts, but it might be argued with equal right that the enzymes may change the properties of the protoplast.

Pfeiffer (1931), who worked with spontaneously freed protoplasts from fruits of *Solanum nigrum*, could find no consistent relation between the volume of the protoplasts and the osmotic value of the medium. However, it is not unlikely that his material was too heterogeneous for an investigation of this kind. Perhaps part of the protoplasts were in a more or less degenerated condition, as Pfeiffer mentions a shrinkage of their surface. In our own experiments such a shrunken surface invariably indicated that the protoplast was on the verge of exploding or of extruding part of its contents.

Since 1918 Seifriz has been studying the structure and the physicochemical properties of the protoplasm, on which he published several papers. In his later work he used isolated protoplasts, and studied their "structural viscosity" and elasticity. In dealing with the protoplasm the term "structural viscosity" (Ostwald, 1925; Philippof, 1935) seems to deserve preference above mere "viscosity", as the use of the latter should be restricted to Newtonian liquids, and the protoplasm certainly does not belong to this category.

Finally Levitt, Scarth and Gibbs (1936) developed the abovementioned micro-cinematographic method for studying the permeability of isolated protoplasts for water, and measured the rate at which the volume changes in solutions of various osmotic value. The solutions containing NaCl and $CaCl_2$ mixtures they used in their experiments, were rather concentrated. It may be that this was the reason why in quite a number of protoplasts the tonoplasts alone survived. This is apparent from their photographs, where the images often do not show either a nucleus or any other recognizable structure and appear as fully transparent spheres, which proves that they are tonoplasts.

§ 3. On the use of the terms "plasmolysis" and "deplasmolysis"

In the present paper we will use the name "gymnoplast" for the isolated protoplasts, a term, which was introduced by Strugger (1948). This, however, is of minor importance, but more is to be said about the use of the terms "plasmolysis" and "deplasmolysis".

In 1899 Balbiani published a paper in which he described how *Paramaecium* passed through several stages of shriveling under the influence of different salt solutions. Balbiani called this phenomenon "plasmorhysis", a term derived from *ῥύσος*, which means shriveling or shrinkage. This term has erroneously been adopted by Küster (1929), Levitt, Scarth and Gibbs (1936) and Koningsberger (1947, b) for the contraction of gymnoplasts in hypertonic media. These authors avoided the use of the terms "plasmolysis" and "deplasmolysis" for gymnoplasts, because "lysis" refers to the disengagement of the protoplasm from the cell wall, which is absent in the gymnoplasts. Since, however, the surface of normal gymnoplasts is perfectly smooth and not shrunken, the use of the terms "plasmorhysis" and "deplasmorhysis" is misleading.

Although it must be admitted that the terms "plasmolysis" and "deplasmolysis" are not fully adequate in describing the changes in volume the gymnoplasts undergo under the influence of media of different osmotic value, they have generally been applied in this field too, and as it does not seem desirable to burden plant physiology with a new technical term, we too have accepted them in the present paper.

Chapter II

Procedure

§ 1. Preparation and handling of material

A. Isolation of gymnoplasts

The onion bulb proved to be the most suitable source of material for our experiments. The bulbs were grown in our garden, and afterwards stored in a refrigerator.

Rahn (1933) found by chemical estimation that onion bulbs in the resting and in the growing period differed considerably in the amount of carbohydrates and of nitrogenous storage materials theyc ontained. A similar seasonal influence also appeared in the experiments of Loeven and Beets (1955) on the permeability of *Allium* cells to water. The latter was found to decrease with the approach of winter, a phenomenon which the authors ascribe to esterification of the phosphoric acid in the phosphatide layer of the plasma-membrane, a hypothesis that found support in a study of Meyer (1957) dealing with the changes the phosphatide fraction undergoes in sprouting onions. In view of these seasonal differences it seemed advisable to take the experiments, in order to obtain readily comparable results, as far as possible in the same months.

Rahn also noted that the contents of bulbscales inserted at various distances from the centre, differ considerably in chemical composition. In our own experiments we used for this reason always a similar set of scales, viz. counted from the periphery towards the centre the scales 3 to 5.

According to Houska (1939) the osmotic value of the cells increases in each scale from the top towards the base. For this reason we always took our material, as far as possible, from the same zone, for which we chose the one midway between top and base. By the aid of a razor we cut here parallel to the surface a slice about 0.15 cm thick and 0.6 by 1.0 cm in extent; a slice of this thickness contains but a small amount of parenchyma, and this, as we will see hereafter, must be regarded as an advantage.

The slices were immersed in a plasmolyte. The latter usually contained 0.66 mol dextrose and in addition potassium and calcium salts in proportions varying according to the season and to the nature of the experiments. In this solution they were left until the protoplasts had freed themselves as far as possible from the cell wall and had assumed a more or less spherical shape. It should however be noted that the plasmolysed protoplasts varied considerably in shape and that there was also a considerable difference in the time they required to assume this shape. This is in agreement with the results obtained by Ruge (1940) and Schaefer (1955), who showed, respectively for *Helodea* and *Lemna*, that the shape of the plasmolysed protoplasts as well as the time it takes to effect plasmolysis, are strongly dependent upon the viscosity of the protoplasm, which in its turn depends upon the proportion in which the Ca- and K-ions are represented in the plasmolyte. Therefore, whenever possible, before starting a series of experiments, the most suitable proportion between these ions was always experimentally determined.

The slices were then transferred to a watch-glass filled with the same solution, and by the aid of dissecting needles parallel to the longitudinal axis of the epidermis cells slowly and carefully cut up under a binocular microscope. This proved to be the more difficult the larger the amount of parenchyma cells that adhered to the epidermis. When the protruding gymnoplasts did not free themselves spontaneously, we helped them a little by tapping the cells with a needle. Dependent upon the salt concentration in the plasmolyte, from 10 to 50 gymnoplasts were set free through each scratch.

B. Transference of the gymnoplasts to the experimental vessel

The gymnoplasts were collected by means of a micro-pipette, fig. 1. Its aperture had a width of circ. 0.4 mm, so that even the largest ones could be sucked up without suffering damage. In order to obviate the danger of a loss of elasticity in the peripheral layers of the protoplasm, sucking up as well as blowing out had to be done with caution. First of all the gymnoplasts were freed, as far as possible, from pollutions derived from the dissected tissue by transferring them to a second watch-glass filled with a solution of the same composition. The washing served not only to facilitate afterwards the observation of the gymnoplasts, but it also protected them against the action of the contents of damaged protoplasts. According to Ziegler (1955) this action, which would be due to the liberation of chemotactically active substances from the wounded cells, would manifest itself in an irregular displacement of the protoplasm along the surface. However, it is not quite clear whether this displacement is distinguishable from a systrophe, i.e. an agglomeration of protoplasm round the nucleus (Germ, 1933). After the gymnoplasts had been cleaned as far as possible, they were transferred with as little water as possible to the experimental vessel; the latter too contained a solution of the same composition. As the amount of fluid that was transferred was very small, the volume of the solution in the experimental vessel remained practically unchanged.

The experimental vessel was circ. 6.5 cm high and had at the top a diameter of 1.7 cm and at the base one of 0.8 cm. The bottom was formed by a cover-glass that had been fixed with araldite. The gymnoplasts were distributed over the bottom by means of the micro-pipette, which to this end was clasped in an adjustable holder (Fig. 1).

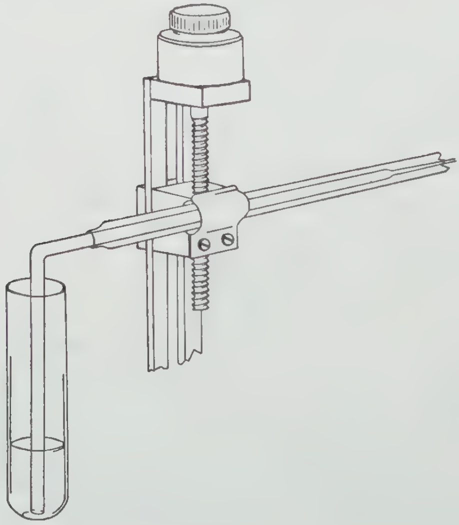

Fig. 1. Adjustable holder with micro-pipette; to the left the experimental vessel

The position of the gymnoplasts could be adjusted by means of a glass rod, and abnormally large and small ones as well as tissue rests could be removed in the same way. Care was taken that the gymnoplasts did not come too close to each other, for during deplasmolysis there should be sufficient space for them to expand without running the risk to come into contact with each other, as that might lead to a fusion.

§ 2. EXPERIMENTAL PROCEDURE

A. *The apparatus*

Our experimental procedure was based on that of KONINGSBERGER *et al.* (1947, b). The alterations we effected in the latter are on the whole of minor importance; one of them, however, is of a somewhat more fundamental nature, and will therefore be shortly described. To increase the reliability of the results, our experiments were not made with a single gymnoplast but with 8 to 20 of them; however, in order to observe the latter at the same time, the size of the field of view had to be increased, which means that we had to work with a low magnification.

For the arrangement of the various parts of the apparatus we refer to Fig. 2 and Fig. 3.

A small perspex basin with a base of 15 by 15 cm and a height of 12 cm served as thermostat. The bottom was perforated by a circular hole (p) fitted out with a rubber ring. In this hole the experimental vessel in which the gymnoplasts had already been deposited, was inserted, the rubber ring ensuring a watertight connection. At the top of the thermostat a brass bridge (b) provided with a brass tube (a) was mounted in such a way that the tube touched the top of the experimental vessel and kept the latter in a vertical position. Up to this tube the thermostat was filled with water. The required temperature was obtained by means of an electrical heating apparatus fixed near the bottom and provided with a lamp (o) serving as resistance, the latter can be seen in Fig. 3. As the gymnoplasts had to be studied by means of a microscope, it was necessary that the bottom of the experimental vessel protruded a little beyond the bottom of the thermostat, and at this place therefore there existed a difference in temperature between the experimental vessel and the environment, which, of course, caused an exchange of heat. However, even if there was a considerable difference in temperature between the two, the increase or decrease of the temperature in the experimental vessel never exceeded 1° C, and as in most experiments the difference in temperature between the experimental vessel and the environment was but small, viz. circ. 5° C, the temperature of the first being 24° C and that of the latter 19° C, the increase or decrease was, as a rule, but insignificant.

An aërating tube (e) provided with a capillary spout could be introduced into the experimental vessel. The tube was clasped in a holder (d), in which it could be moved in a vertical direction by means of a screw. The holder was mounted on an adjustable stage (c) whose movements were regulated by means of two screws (d′ and d″). A horizontal displacement could be obtained by means of the bridge (b) to which the stage was attached. The capillary spout (e) had to be kept as far away as possible from the gymnoplasts in order to avoid the risk that they would be blown away. As it was desirable that the fluid at the bottom too was set in motion, the tube had to be brought down as near as possible to the latter. This manner of stirring had the advantage that the respiration of the gymnoplasts could proceed regularly, as O_2-deficiency as well as a CO_2-surplus was

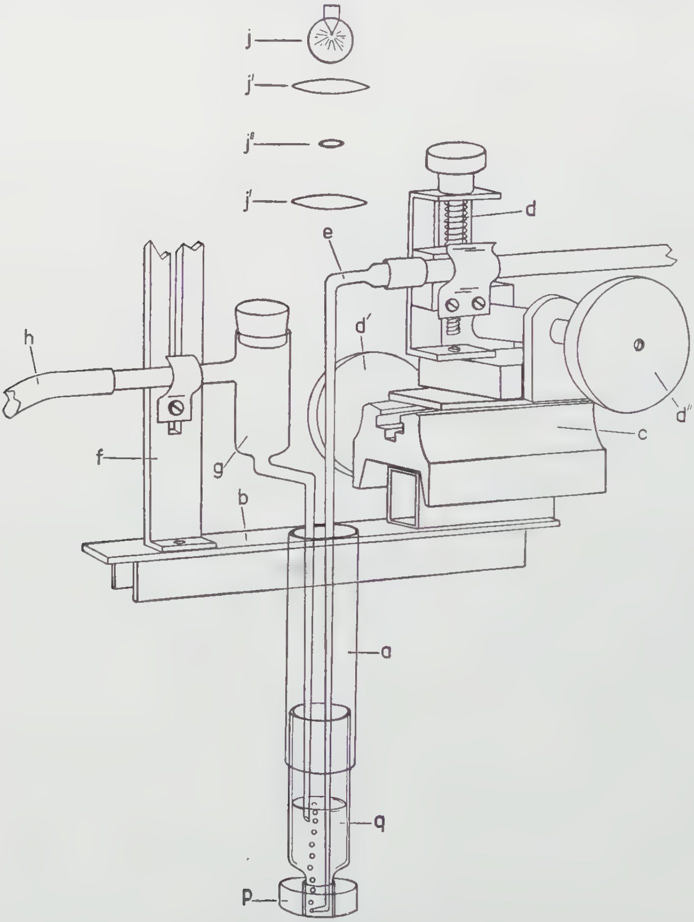

Fig. 2. Parts of the apparatus in or near the thermostat
a. tube by which the experimental vessel is kept in position; b. bridge on top of thermostat; c. adjustable stage; d. holder for aerating tube; d′ and d″. screws for adjusting position of stage; e. aerating tube; f. holder for filling tube; g. filling tube; j. lamp; j′. lenses; j″. diaphragm; p. perforation in bottom of thermostat; q. experimental vessel fitting with its base in p.

prevented. We ourselves did not study the respiration, but the experiments of KECKWICK and HARVEY (1934) and those of MEYER and BERNFELD (1946) make it probable that it may affect the reaction of the cells, especially because of the CO_2-production; CO_2 would be able to exercise an influence on the plasma-membrane because of the latter's sensitivity to changes of the pH. The air that was blown through the aerating tube was purified by passing it through a flask containing concentrated sulphuric acid.

In order to be able to change the composition of the solution in the experimental vessel, we had at our disposition a glass tube (g) mounted in a holder (f) and adjustable by means of a screw in a vertical direction. The capillary spout of the empty tube was brought

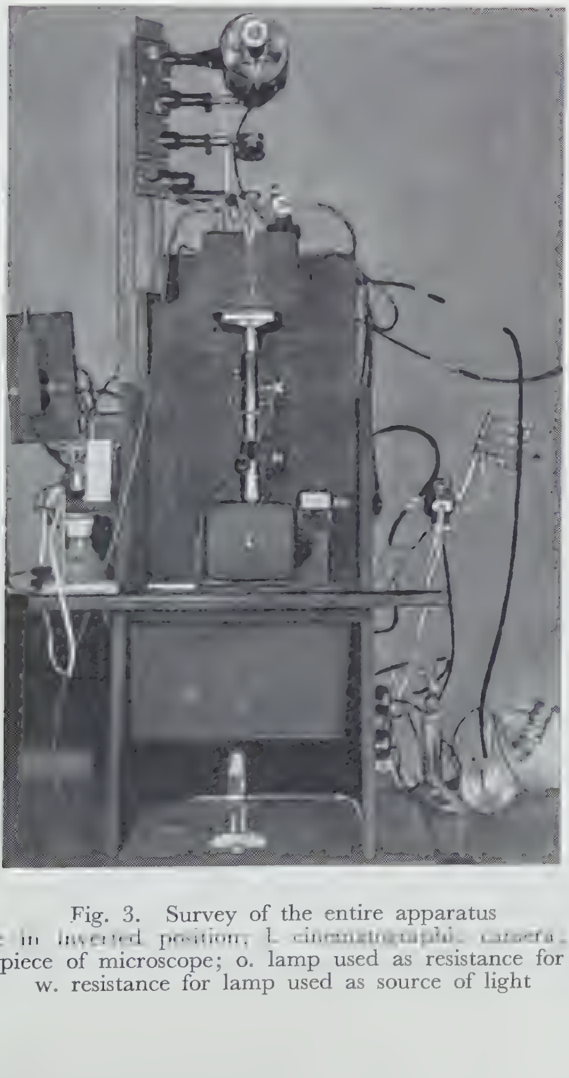

Fig. 3. Survey of the entire apparatus
h. microscope in inverted position; l. cinematographic camera; m. focussing prism; n. eyepiece of microscope; o. lamp used as resistance for heating coil; w. resistance for lamp used as source of light

just below the surface of the fluid, so that the latter could mount slightly in the spout. Then the tube was cautiously filled with the diluting fluid, which remained suspended on a short column of air above the fluid that had mounted in the capillary spout. By blowing through the rubber tube (h) it was at any moment possible to transfer the diluting fluid to the experimental vessel. The width of the capillary spout was chosen in such a way that the fluid could be blown out of the tube within the space of a minute but without causing a disturbance that would displace the gymnoplasts.

The thermostat with its accessory parts stood on the stage of an inverted microscope (k), Fig. 3, whose pedestal was fastened to a vertical board and whose diaphragm and condensor had been removed in order to allow the observation of the gymnoplasts through the opening in the stage.

The gymnoplasts could be photographed by means of a cinematographic camera (l) and simultaneously observed through the (horizontal) ocular (n). They were illuminated by means of a Philips lamp of the type 12V-100W-HH (j), Fig. 2, which was very suitable for this purpose because of its tightly wound glow spiral. The light intensity was regulated by the aid of a system of lenses (j′), a diaphragm (j″) and a resistance (w), Fig. 3. The lamp was surrounded by a cylinder connected with an air-cooling motor, which absorbed its lateral radiation of light and heat. Lamp and lenses were mounted on an optical bench.

To obtain a sharp image of the gymnoplasts a focussing prism (m), Fig. 3, was used; the latter was mounted on the camera at the same level as the film. In order to bring the prism under the microscope, the film camera had to be removed; this was done along rails.

The amount of light used for focussing as well as that used for photographing had to be kept as low as possible, as it seemed undesirable to expose the gymnoplasts unnecessarily to light. In the literature several examples are to be found of plant cells of which the protoplasm is influenced by light, e.g those of *Valonia* (Brooks, 1927), *Helodea* (Virgin, 1951/52), and *Allium* (Biebl, 1942). In the first two objects the influence may be exercised by the intermediary of the chlorophyll system, but in the epiderm of the onion scales it will be of a different kind.

The cinematographic camera was connected with an intermittent clinostat (type de Bouter), which was adjusted in such a way that it took 1 to 3 minutes to complete a revolution. Aëration and illumination were automatically regulated by means of the same synchronic motor. Every time a photograph had to be taken, this motor interrupted the aëration, so that the gymnoplasts came to rest; after that the shutter was opened by the clinostat. Next the synchronic motor made the lamp burn for circ. two seconds, in which time the photograph was taken. Then the shutter was closed by the clinostat, and the exposed part of the film passed on; at the same time the aëration was restored by the synchronic motor. In this way it requires circ. 10 seconds before the next photograph can be taken. When necessary, the camera could also be worked by hand.

The aëration of the experimental vessel was automatically regulated by means of an electro-magnet, Fig. 4 (1). On a motile piece of cast iron (2) small brass plates (3, 3′) were mounted. Between the latter narrow and thin rubber tubes were fixed which served respectively for admitting (4) and expulsing (8) air. These tubes were connected with two of the ramifications of a three-forked piece of glass tubing, the third ramification leading via another rubber tube to the glass tube by which the experimental vessel was aërated. So long as there ran no current through the electro-magnet, the piece of cast iron was, by the aid of adjustable springs (5), drawn towards the brass rod (9′), and then the passage through the narrow rubber tube (8) which served as exit for the air was blocked by the brass plate (3′), so that the air that was admitted through the other narrow tube (4) went to the aërating tube. The latter was put out of action when the electro-magnet attracted the motile piece of cast iron, for then the passage through the narrow rubber tube (4) which served for the entrance of air, was blocked because of the pressure exercised on it by the brass plate (3) and the brass rod (9). The passage through the narrow rubber tube (8) which served as exit for the air, was at the same time reopened; this was necessary in order to find a means for evacuating the surplus air in the aërating tube into the experimental vessel; in this way we prevented that the pressure in the aërating tube would become too high when the passage through the latter was reopened; this would result into a sudden discharge of

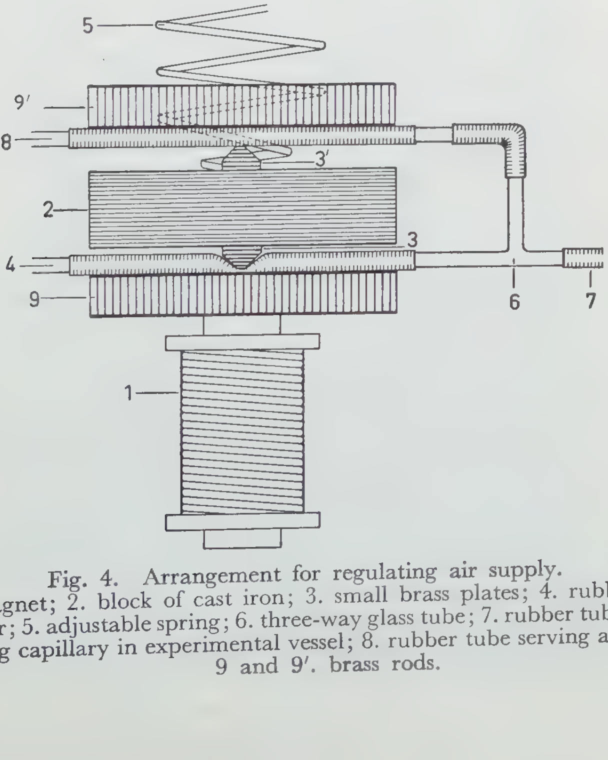

Fig. 4. Arrangement for regulating air supply.
1. electromagnet; 2. block of cast iron; 3. small brass plates; 4. rubber tube for admitting air; 5. adjustable spring; 6. three-way glass tube; 7. rubber tube connected with aerating capillary in experimental vessel; 8. rubber tube serving as exit of air; 9 and 9′. brass rods.

air into the experimental vessel; by such a discharge the gymnoplasts would be blown away.

The photographs were taken on an Agfa duplo-orthofilm, and they were developed by means of a borax fine-grain developer prepared according to prescription G 206 of Craeijbeck (1950).

B. The way in which the experiments were taken

After a sharp image of the gymnoplasts, which at that moment were still immersed in the plasmolyte, had been obtained in the focussing prism, and could therefore also be expected on the film, the camera was shifted backwards until its opening stood just below the ocular of the microscope; then two photographs were taken. The synchronic motor was in this case adjusted in such a way that every minute a photograph could be taken. Immediately after these photographs, which would have to serve as norm, had been taken, the film was turned the space of one image further, in order to mark this point, the synchronic motor in the meantime continuing to revolve at the same rate. After this the fluid in which the behaviour of the gymnoplasts was to be studied, was blown into the experimental vessel in such a way that the transference of this fluid was completed before the next photograph was taken by the aid of the synchronic motor. During the next two minutes air was blown through the tube (h), Fig. 2, in order to accelerate the mixing of the two fluids. For circ. twelve minutes the motor continued to revolve at the same rate. After that the film was once more turned the space of one image further, and the synchronic motor adjusted in such a way that instead of every minute every three minutes a photograph could be taken; this rate was kept up until the experiment had gone on for circ. 35 minutes. The length of the various periods could, of course, be changed when, as in our study of the temperature influence, this was required by the nature of the experiments.

C. The way in which the gymnoplasts were measured and that in which the results were put down in the form of a graph

A Leitz projector for diapositives of 5 by 5 cm proved very suitable for projecting the films on a flat sheet of white paper. The gymnoplasts appeared on the screen in the form of circles with a diameter of 70 to 200 mm (Fig. 5). As their actual diameter varies according to measurements performed on 36 individuals from 46 to 120 μ, the magnification is circ. 1500. In order to facilitate comparison of the gymnoplasts in the successive projections, each individual gymnoplast received a number. Those that were to be used for our purpose, had to show a characteristic structural element, preferably a nucleus, otherwise we could not be sure that they really represented a complete gymnoplast and not merely a tonoplast. When this certainty had been obtained, the gymnoplasts were measured along various diameters. This was done in order to find out whether the projection might be regarded as approximately circular. When the difference between two of the diameters exceeded 2 %, the gymnoplast was discarded. The measuring error appeared to be circ. 0.4 %.

That the gymnoplasts possess a spherical form, is to be regarded as a necessary condition for the application of our method. However, a perfectly circular image on the screen does not a priori prove that the gymnoplast really is spherical; it might just as well have the form of an ellipsoid, e.g. because of compression in a direction vertical to the screen. When such a compression, which might be due to a flaccid condition of the gymnoplast, were present, our method would lead to entirely unreliable results.

When we had accidentally obtained some indications that in certain media, viz. in solutions of dextrose which did not contain salts, such compressions really occur, we decided to devote a special study to this problem.

To this end we plasmolysed tissue of onion scales and isolated the

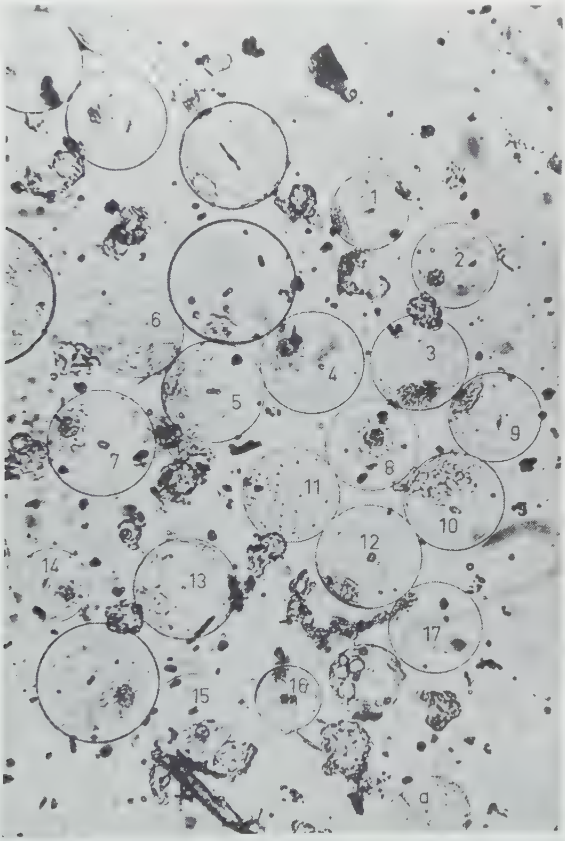

Fig. 5. Gymnoplasts seen in projection on screen. The numbered gymnoplasts are those that could be used. a. fusion between two gymnoplasts.

gymnoplasts a) in a 0.66 mol dextrose solution, b) in a 0.66 mol dextrose solution containing in addition 0.1 n KCl, and c) in a 0.66 mol. dextrose solution with in addition 0.05 n KCl and 0.05 n $CaCl_2$. Subsequently the gymnoplasts were transferred to a perspex vessel with a content of 2 ml and filled with the solution in which they had been plasmolysed. The bottom of this vessel was covered with a glass slide, so that the substrate on which the gymnoplasts rested was the same as in the other experiments. This vessel was placed on a small beam which was fastened to the stage of a microscope. The latter was laid horizontal so that the gymnoplasts were seen from the side instead of from below as in our other experiments. After they had been photographed, they were projected on the screen and their two most strongly deviating diameters measured. The results of these measurements are given in Table I.

When we make it a condition that the difference in diameter must not exceed 2 %, it appears that not a single one of the gymnoplasts that had been plasmolysed in the dextrose solution without salts, can be used. Addition of 0.1 n KCl to the plasmolyte gives a much better result, for now in 80 % of the gymnoplasts the difference between the diameters appears to remain within the admissible limits, and in the solution in which to the dextrose 0.05 n KCl and 0.05 n $CaCl_2$ had been added, it appears that practically all gymnoplasts may for our purpose be regarded as perfectly spherical.

It is therefore not allowed to work with a plasmolyte consisting of dextrose only, as in such a solution all gymnoplasts become flaccid. However, as soon as ions are present, the gymnoplasts attain a higher degree of elasticity, so that they are able to assume a spherical shape. Especially when Ca- as well as K-ions are present, the consistency of the protoplasm is such that nearly all gymnoplasts show the spherical shape. This is in agreement with the observations of Ponder-Saslow (1930/31) on the shape of erythrocytes, which is discoid in an environment that is poor in salts, but becomes spherical in a solution containing K- and Ca-ions.

It has unfortunately not been possible to photograph the same gymnoplast from below as well as from the side, but it seems plausible to assume that the gymnoplasts we used in our experiments really possessed a spherical shape, as our dextrose solutions always contained in addition K- and Ca-ions, and as the only other fluids with which we worked were solutions of 0.1 n KCl or of 0.1 n $CaCl_2$.

Our observations on gymnoplasts that were kept in dextrose solutions not containing any ions, have moreover taught us that the deformation is not confined to a flattening in the direction of the vertical axis but that it affects the whole form, which becomes more or less irregular.

In the experiments which will be described further on, including those in which the solution contained but one kind of cation, the chance that we might arrive, on account of irregularities in the shape of the gymnoplasts, to erroneous conclusions, is therefore very small indeed. The difference between the horizontal and the vertical dia-

Table I

Approximately horizontal (I) and vertical (II) diameters of gymnoplasts plasmolysed respectively in solutions of 0.66 mol dextrose (*a*), 0.66 mol dextrose + 0.1 n KCl (*b*), and 0.66 mol dextrose + 0.05 n KCl + 0.05 n $CaCl_2$ (*c*). The gymnoplasts plasmolysed in the solutions (*b*) and (*c*) are arranged in groups according to the magnitude of the difference between the two diameters expressed as a percentage of the horizontal one.

Plasmolyte	*a*: 0.66 mol dextrose		*b*: 0.66 mol dextrose + 0.1 n KCl										*c*: 0.66 mol dextr. + 0.05 n KCl + 0.05 n $CaCl_2$			
Difference between the two diameters expressed as a percentage	4.5–22.5		0		0–1		1–2		2–4		4		0		0–2	
Diameter in mm as measured in the projection on the screen	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
	130	124	130	130	124	123	136	134	120 1)	124	95 1)	100	125	125	138	137
	131	123	122	122	119	120	135	133	130	127	106 1)	130	136	136	129	127
	120 1)	155	124	124	107	108	121	119	139 1)	142			124	124	142	140
	159	137	157	157	177	178	114	112	144	139			151	151	158	157
	132	125	172	172	120	119	104	102	135	132			140	140		
			124	124	138	137	138	136	97	95			129	129		
			127	127	172	173	125	123	100	98			137	137		
			125	125	128	127	119	121	124	120			119	119		
			175	175	172	173	155	152	128	125			161	161		
			86	86	138	139	126	128	145 1)	148			138	138		
			125	125	151	152	140	138					109	109		
			160	160	77	76							117	117		
			127	127	136	137							129	129		
			145	145	134	135										
			119	119	124	123										
			140	140	176	177										
					139	138										
					131	130										
					149	150										
					136	135										
					122	121										
percentage of gymnoplasts in each group	100		27.42		33.87		19.35		16.13		3.23		76.42		23.58	

1) In these gymnoplasts the horizontal diameter was significantly smaller than the vertical one.

meter we found in solutions containing KCl is to be ascribed to a slight flattening on the side that is in contact with the bottom of the vessel. By setting aside all gymnoplasts showing in the projection on the screen deviations from the circular outline, we will most probably have succeeded in eliminating all those that are not perfectly spherical. However, the number of gymnoplasts that had to be discarded for this reason, was sometimes very large, viz. up to 50 %. Gymnoplasts that in the course of the experiment began to show irregularities in their shape, were also put aside.

To determine the degree of permeability for water, the solution in which the gymnoplasts had been plasmolysed, had to be diluted. A measure for this permeability is found in the relative increase in diameter shown by the gymnoplasts in the unit of time.

When in the projections on the screen the diameter of the gymnoplasts in the successive stages had been measured, the values for the increase were determined and, expressed as a percentage of the average initial diameter, set down in the form of a graph. The data used for the construction of the graph shown in Fig. 6, were obtained in the experiments 1 and 2, the first experiments to give good results. In Table II under *a*, moreover, for experiment 1 the absolute value of the initial and of the final diameter measured in the projection of the nine gymnoplasts on the screen, are set down, whereas under *b* in this table the increase in diameter of the same nine gymnoplasts expressed as a percentage of the initial value is given.

The increase in diameter does not always proceed in a regular way. It even happens that it temporarily stops. Circ. 55 % of the gymnoplasts appear to reach the state of equilibrium within 20 minutes,

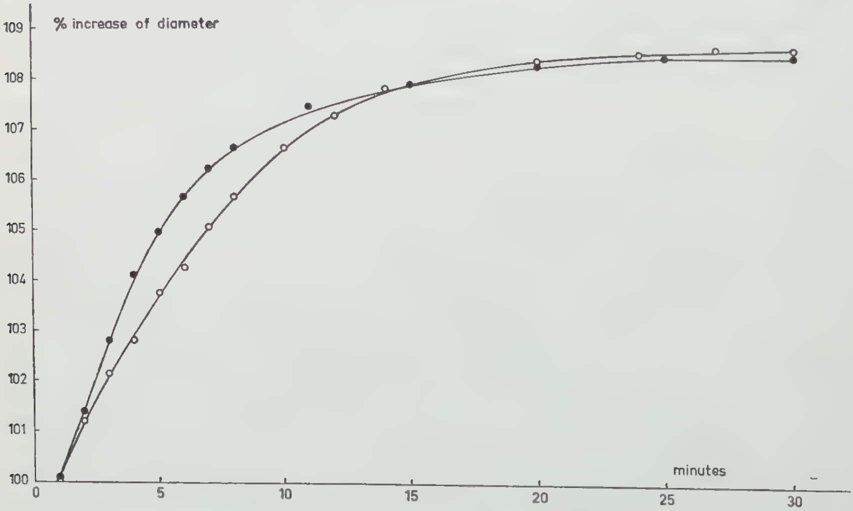

Fig. 6. Subsequent stages of deplasmolysis. The experimental vessel contained 1.6 ml of a solution of 0.66 mol dextrose, 0.04 n KNO_3 and 0.045 n $CaCl_2$. Deplasmolysis was obtained by adding 0.6 ml aq. dest. Temp. 24° C. ○ experiment 1; ● experiment 2.

TABLE II

Progress of deplasmolysis. The 1.6 ml solution in the experimental vessel contained 0.66 mol dextrose, 0.04 n KNO_3 and 0.045 n $CaCl_2$. Deplasmolysis was obtained by adding 0.6 ml aq. dest. Temp. 24° C.

a. Initial and final diameter of the nine individual gymnoplasts of experiment 1

gymnoplast number	1	2	3	4	5	6	7	8	9	average
initial diameter of the image on the screen in mm	78	98	95.5	158	121	109	128	146	925	$114.1 \pm 8.81 (r_0)$
final diameter of same . . .	86	106	104	172·5	131	118	139	158	100	$123.8 \pm 9.54 (r_\infty)$

b. Increase in diameter in the same nine gymnoplasts expressed as a percentage of the initial value

gymnoplast number	1	2	3	4	5	6	7	8	9	average diameter as a percentage of initial value
0 min.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100
1 min.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100
2 min.	3.16	1.02	1.57	1.26	1.65	0.91	0.78	0.68	0.54	101.22 ± 0.80
3 min.	3.79	2.04	2.61	1.89	2.47	1.82	2.34	2.04	1.62	102.14 ± 0.66
4 min.	3.70	2.04	3.66	2.52	3.36	2.73	2.34	2.72	2.70	102.82 ± 0.53
5 min.	5.06	3.06	4.18	3.79	4.13	3.64	3.90	4.08	3.78	103.75 ± 0.66
6 min.	5.06	3.57	4.71	3.79	4.13	4.55	3.90	4.76	4.86	104.24 ± 0.51
7 min.	6.32	4.08	4.71	5.06	4.95	5.46	4.68	5.44	5.94	105.06 ± 0.70
8 min.	6.32	5.10	5.74	5.69	5.78	5.46	5.46	6.86	5.94	105.65 ± 0.34
10 min.	7.59	5.10	6.80	6.96	6.63	6.37	6.24	6.86	7.02	106.42 ± 0.45
12 min.	7.59	5.61	6.80	8.22	6.63	7.28	7.02	7.52	7.02	107.25 ± 0.72
15 min.	7.59	6 12	7.85	9.17	7.46	8.19	7.80	8.96	8.11	107.79 ± 0.81
20 min.	7.59	6.12	7.85	10.12	8.26	8.19	8.59	8.22	8.11	108.33 ± 0.91
24 min.	8.22	7.14	8.90	9.17	8.26	8.19	8.59	8.22	8.11	108.42 ± 0.58
27 min.	8.22	8.17	8.90	9.17	8.26	8.19	8.59	8.22	8.11	108.52 ± 0.39
30 min.	8.22	8.17	8.90	9.17	8.26	8.19	8.59	8.22	8.11	108.52 ± 0.39

and the remaining ones arrive at this stage within 24 to 27 minutes. This period of rest lasts a considerable time, for even after 45 minutes no further changes were noted. Half an hour therefore proved to be sufficient for obtaining a satisfactory record of the reaction. When it appeared that a gymnoplast had not reached the state of equilibrium within that time, it was left out of consideration.

§ 3. MATHEMATICAL ANALYSIS

The two graphs shown in Fig. 6 do not give us a clear idea of the velocity with which water penetrates into the expanding gymnoplast, i.e. of the latter's degree of permeability. For this reason we went in search of an equally objective but at the same time more readily comprehensible way of expressing this function of the gymnoplasts. It was arrived at by way of the following considerations ¹).

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¹) For the development of the analytical method expounded in the following pages and for a large part of the calculations involved in its application I am indebted to Dr D. DE JONG, to whom I tender my best thanks.

As the volume V of a spherical gymnoplast with a radius r is $\frac{4}{3}\pi r^3$, the change of volume dependent on time is

$$\frac{dV}{dt} = 4\pi r^2 \frac{dr}{dt} \tag{1}$$

As the surface S of the gymnoplast is $4\pi r^2$, this equation may also be written in the form

$$\frac{1}{S} \times \frac{dV}{dt} = \frac{dr}{dt} \tag{2}$$

Eq. (2) gives us the amount of water which passes, in one direction or the other, the unit of surface in the unit of time. The factor in which we are especially interested, the permeation through the unit of surface, therefore is directly measurable as a change in diameter ($2r$).

By the introduction of a constant the above relation could be made valid also for gymnoplasts possessing another shape, e.g. an ellipsoidal one, provided that the shape does not change during the change of volume, and that the increase or decrease in diameter is studied in projections obtained in the same direction.

On account of the permeability of the protoplasm for water the volume of a gymnoplast will undergo a change when the latter is transferred to a solution with a different concentration. However, as the protoplasm offers a certain resistance to the passage of water, it will take some time before the initial volume V_0 of a spherical gymnoplast with the radius r_0 has reached the final V_p and before its radius has become r_p; when the way in which this change takes place may be regarded as an exponential function, the final stage is, strictly speaking, reached only after an indefinitely long time. For this reason we will in the following part of our exposition represent the final volume by the symbol V_∞ and the radius of the sphere by r_∞.

A simple supposition, which would seem to be independent of any special notion we might have as to the mechanism involved, is that the velocity with which the change of r takes place, is directly proportional to the difference between its present value and the ultimate one:

$$\frac{dr}{dt} = \frac{l}{\tau_e}(r_\infty - r)$$

in which τ_e is a constant with a time dimension.

The solution of this equation gives us, assuming that our supposition is acceptable, the relation between r and t. It is

$$r = r_0\, e^{(-t/\tau_e)} + r_\infty\,(1 - e^{(-t/\tau_e)}) \tag{3}$$

This solution fulfils the three essential conditions: it is in agreement with the differential equation; when $t = 0$, $r = r_0$; and when $t = \infty$, $r = r_\infty$.

The Eq. (3) may also be written in the following form

$$\frac{r_\infty - r}{r_0} = \frac{r_\infty -}{r_0}\, e^{(-t/\tau e)} \tag{3a}$$

Here the left member of the equation represents the change of r that still has to take place, whereas the factor $\frac{r_\infty - r_0}{r_0}$ in the right member represents the total change of r (the difference between its initial and ultimate value), both expressed as a fraction of the initial value.

When we assume that

$$r_\infty - r = p\ r_0 \text{ and } r_\infty - r_0 = p_0\ r_0$$

we obtain

$$p = p_0\ e^{(-t/\tau_e)} \tag{3b}$$

Therefore, when r increases from r_0 to r_∞, p decreases exponentially from p_0 to 0.

The time constant τ_e here represents the time in which r has decreased with a factor e, i.e. in which it has undergone 63.2 % of the total change.

When we replace τ_e by another, more usual time constant, viz. by $\tau = \tau_e \log 2/ \log e$, the Eq. (3b) becomes

$$p = p_0 \cdot 2^{(-t/\tau)} \tag{3c}$$

In this way the meaning of the time constant becomes more obvious; τ here represents the time in which r achieves half the total change; this τ therefore is the "half-value-constant", h.v.c., a time function. The shorter this h.v.c. the greater the permeability.

In the Eq. (3b) $p_0 = \frac{r_\infty - r_0}{r_0}$ is the "total relative increase of r", or $100 . p_0$ is the "total increase of r expressed as a percentage" and $100 . p$ the "still to be achieved increase of r expressed as a percentage".

Now when working out a series of measurements, we determine first of all p_0 by means of the equation $p_0 = \frac{r_\infty - r_0}{r_0}$; after that we determine for every r_t the corresponding p_t. The values obtained in this way are used for the construction of a graph in which the value for $\log p = - \frac{t}{\tau} \log 2 + \log p_0$ is set out as a function of the time t. The easiest way to do this is to take simple logarithmic paper provided with a linear time scale. In Fig. 7 the values of $100\,p$ are plotted for simplicity instead of those of p. If we leave the first period of circ. 2 minutes out of consideration, these graphs appear to have the form of straight lines.

The initial phase of circ. 2 minutes is not of essential importance, as time zero we choose the moment at which a tangent to the steepest part of the curve cuts the X-axis. In Fig. 6 the corrected value for time zero is 0.7 min. The point that is comparable with 1 min. in Fig. 7 therefore is 1.7 min. The diameter pertaining to this corrected point t_1 is r_1.

The real time zero is apparently not the beginning of the deplasmolysis, and this was to be expected as the diluting fluid and the plasmolyte are not at once completely mixed. The point on the X-axis obtained by extrapolating the rectilinear part of the curve will therefore in all probability be a closer approximation of the real starting point.

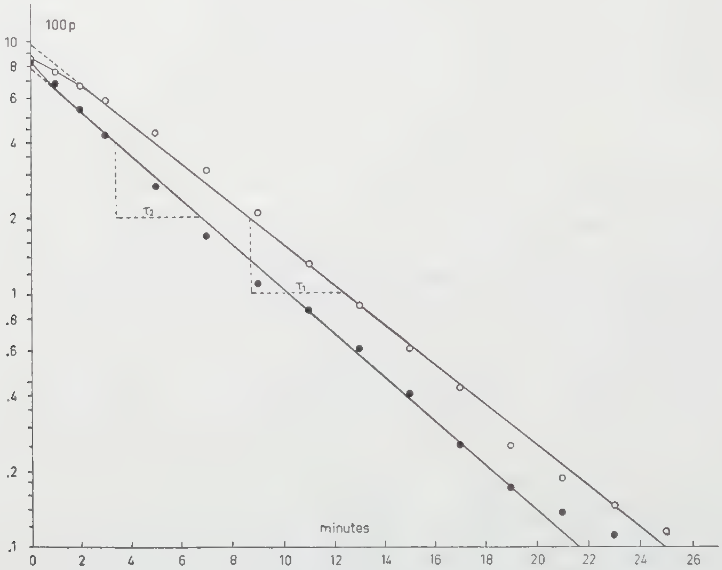

Fig. 7. Estimation of h.v.c., i.e. the time required to achieve half the total decrease. Experimental conditions and symbols as sub Fig. 6. $\tau_1 = 3.70$ min.; $\tau_2 = 3.40$ min.

From the preceding considerations we may conclude that the method based on the supposition which led to the differential equation

$$\frac{dr}{dt} = \frac{1}{\tau_e} (r_\infty - r)$$

enables us to express the results of our experiments with the aid o two parameters, viz. the relative total increase of the diameter p_0, and the "half-value constant" τ. In p_0 we recognize the static properties of the plasma membrane, in τ the latter's dynamic properties (e.g. the percolation resistance).

If we use the method expounded above in order to determine the h.v.c. in experiment 1, we find for it 3.70 min. This therefore is the time required for reducing a difference in diameter of 4 % to one of 2 %. The accuracy with which we can determine h.v.c. from this figure is ± 0.05 min.

§ 4. CRITICAL CONSIDERATIONS

We will now have to find out whether the parameters p_0 and τ (=h.v.c.) are independent of the size of the gymnoplasts, for if they varied with the latter, it would not be allowed to average the diameters of a set of gymnoplasts, but we would be compelled to divide the latter according to their size in different groups.

As the parameter p_0 introduced in the preceding section of this chapter was determined by means of the formula $\frac{r_\infty - r_0}{r_0}$ we will have to find out whether the increase of r_0 to r_∞ expressed as a percentage of r_0 might not depend on the absolute value of r_0. In order to find a reliable answer to this question we have determined the correlation between the total increase of the diameter expressed as a percentage of the initial value and the absolute value of the initial diameter of the various individuals. We did this by means of the correlation coefficient, and the values for the latter found in five different experiments are given in Table III. The data used for calculating this coefficient for the nine individual gymnoplasts of experiment 1 have been given in Table IIa.

TABLE III

Correlation between the magnitude of the ultimate diameter and the initial diameter of individual gymnoplasts as measured by means of the correlation coefficient. The experimental vessel contained 1.6 ml of a solution of 0.66 mol dextrose, 0.04 n KNO_3 and 0.045 n $CaCl_2$. Deplasmolysis was obtained by diluting with 0.6 ml aq. dest. Temp. 24° C.

exp.	number of gymnoplasts	correlation coefficient
1	9	0.35
2	13	0.48
3	15	0.34
4	12	0.19
5	16	0.36

All correlation coefficients prove to be less than 0.5. We may therefore conclude that the relative increase of the diameter of the gymnoplasts is, in general, independent of the original size of the latter, and it is therefore admissible to use the average relative increase of gymnoplasts differing in their original size as a general measure of the increase. However, as in experiment 2 of Table III the correlation coefficient proves to be a bit high, it seems advisable to avoid the use of very large as well as of very small gymnoplasts. An example of such a slight correlation is seen in fig. 8, where the value of the total increase in diameter expressed as a percentage of the initial one has been set out as a function of the latter.

In order to find out whether the parameter τ (h.v.c.) is independent of the initial size of the gymnoplasts we will have to see whether there exists a correlation between the absolute length of the initial diameter of the gymnoplasts and the rate at which deplasmolysis proceeds in each of them. To this end we determined the correlation between the inclination of the tangent drawn to the steepest part of the deplasmolysis graphs and the initial diameter of the individual gymnoplasts. The results expressed by means of the correlation coefficient are given in Table IV.

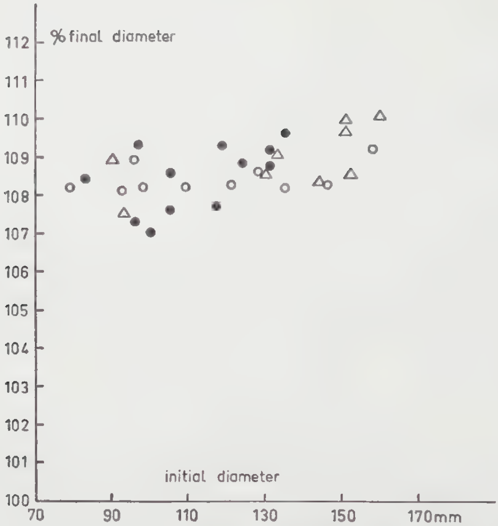

Fig. 8. Diagram showing the correlation between the relative value of the final diameter and the absolute value of the initial one. Experimental conditions as sub Fig. 6.

Table IV

Correlation between rate of deplasmolysis (the inclination of the tangent drawn to the steepest part of the deplasmolysis graph) and magnitude of the initial diameter of individual gymnoplasts as measured by means of the correlation coefficient. The figures relate to the same experiments as those of Table III.

exp.	number of gymnoplasts	correlation coefficient
1	9	0.22
2	13	0.11
3	15	0.18

The data used for calculating the correlation coefficient for the nine individual gymnoplasts of experiment 1 have been given in Table IIb.

As the correlation coefficients are all three small, it is here too allowed to average the values found for the rate of deplasmolysis in individual gymnoplasts with a different initial diameter, and when it is permissible to average these values, which, as we have seen, find their expression in the "inclination", it is, on account of the direct relation between the "inclination" and the h.v.c., obviously also allowed to average the latter.

The h.v.c. graphs, which, as we have seen, are based on the deplasmolysis graphs, i.e. on the graphs illustrating the relative changes in diameter of the gymnoplasts, appear to show sometimes at the beginning and at the end deviations from the rectilinear course. The beginning and the end, however, are points that have to be determined as accurately as possible, as the first corresponds with the time zero at which theoretically, viz. if the mixing of the plasmolyte and the diluting fluid could have been completed instantaneously, the reaction would have begun, and as the second corresponds with the state of equilibrium.

The h.v.c. is calculated from the difference ($r_\infty - r_t$) as function of the time t. It will be clear that the accuracy of the result of this calculation depends not only on the accuracy with which the various values of r_t are determined but also, and even to a higher degree, on that with which r_∞ can be measured, as the latter affects the position of every point of the graph. In order to obtain some idea of the way in which the h.v.c. depends upon the value accepted for r_∞, we have calculated it in two of our experiments also for values of r_∞ differing 0.1 % from those that were actually measured. The results of these calculations are given in Table V. In every instance the graph constructed on the base of the chosen value proved to be a good approximation to a straight line.

TABLE V

Influence exercised on the value of the h.v.c. by an error of 0.1 % made in measuring the final diameter. The figures relate to the same experiments as those of Table II

Exp. 1		Exp. 2	
r_∞ as a percentage of r_0	the h.v.c.	r_∞ as a percentage of r_0	the h.v.c.
108.40	3.60 min.	108.25	3.25 min.
108.50 (measured)	3.70	108.35 (measured)	3.40
108.60	3.95	108.45	3.60

When we go out from values for r_∞ that fall outside the range observed in our experiments, we obtain graphs which, expressed in logarithmic form, deviate considerably from a rectilinear course.

As plasmolysis as well as deplasmolysis rest on osmosis, which is a kind of diffusion, they will have to obey Fick's law of diffusion. Fick's formula applies to the unit of surface, and it assumes therefore that the latter remains constant; in the gymnoplasts, however, the surface increases in the course of deplasmolysis. Fick's formula shows that diffusion is proportional to the size of the surface through which it takes place, and the increase in size, the surface of our gymnoplasts undergoes in the unit of time, may therefore be regarded as a measure for the rate with which water permeates into the gymnoplast. Instead of the increase in size of the surface we may take the increase in diameter of the gymnoplasts, for so long as the increase in volume is small, and this applies here, the increase in surface area may be regarded as directly proportional to the increase in diameter.

In order that we may apply Fick's formula to the process of endosmosis, the concentration gradient has to be uniform. For this reason the mixing of the two fluids at the beginning of the experiment has to take place rapidly and it has to be complete. The first part of the deplasmolysis graph (Fig. 6) shows us, as we have already noted, in how far this condition has been fulfilled. With the amount and the concentration of the plasmolyte and the amount of diluting fluid that, as a rule, were used by us, we obtained within the first three minutes an increase in diameter of 1 %. When a smaller amount of the diluting fluid was used, this required somewhat more time, with a larger amount somewhat less time.

It is perhaps worthwhile to devote here some attention to another feature that plays a part in the increase in volume of the gymnoplast, viz. the resistance which the diffusion stream experiences in the successive layers of the protoplast: the ectoplasm, the cytoplasm proper and the tonoplast.

The thickness of this system will, of course, be of importance, and also whether and in how far the latter decreases during deplasmolysis. PFEIFFER (1936) seems to be the only author who has given some data with regard to the diameter of the cytoplasm layer; in naked protoplasts obtained from the fruits of *Solanum* species it would be circ. 14 % of the total diameter of the gymnoplast. His exposition, however, is not very clear. Compared with the total thickness of the layer of cytoplasm, that of the ectoplasm and that of the tonoplast are negligible. According to some authors (HANSTEEN CRANNER, GRAFE and MAGISTRIS (1922–1926), GORTER and GRENDEL (1926), HARVEY–DANIELLI (1936), HÖFLER (1951), HOFMEISTER (1954), etc.) these layers would consist of four monomulecular strata formed by lecithin-like compounds and proteins.

Changes in thickness of the cytoplasm layer, therefore, will in the first place be due to changes in thickness of the central layer. Some authors ascribe the difference between the time it takes to obtain plasmolysis and that which is required for deplasmolysis, i.e. the difference in rate between exosmosis and endosmosis, to such a change in thickness of the cytoplasm layer. This, however, does not look very probable.

HÖFLER (1930), HUBER and HÖFLER (1930), LEVITT, SCARTH and GIBBS (1936) and KAMIYA and TAZAWA (1956) have studied this difference in rate between exosmosis and endosmosis, but none of them regards the thickness of the cytoplasm layer as an important factor. In their investigations the time required to obtain plasmolysis and deplasmolysis is, as a rule, taken as a measure of the rate of exosmosis and of endosmosis, and as deplasmolysis takes much less time than plasmolysis, endosmosis is said to proceed at a much faster rate. During plasmolysis the thickness of the cytoplasm layer must increase, whereas during deplasmolysis it becomes thinner. The thickness of this layer therefore might play a part.

However, that the rate of exosmosis and of endosmosis would really be influenced by the thickness of the cytoplasm layer, becomes improbable in face of the results obtained by Kamyia and Tazawa in their experiments with *Nitella*. In non-plasmolyzed, intact internodal cells of the latter, these authors found differences between the rate of exosmosis and of endosmosis which, expressed as a percentage, proved to be of the same order of magnitude as those that were observed in other objects. The absolute value of the rate of exosmosis and of endosmosis, however, was, on the other hand, in their experiments much higher than in those of Levitt *et al.*

Kamiya and Tazawa give a table (*l.c.* p. 418) in which they have brought together the results of their own experiments with those of other authors, and it looks as if this table allows but one conclusion, viz. that for explaining the permeability of the protoplast for water and the differences in the rate at which exosmosis and endosmosis take place, the structure of the system formed by ectoplasm, cytoplasm proper and tonoplast, and the changes this system undergoes during plasmolysis and deplasmolysis, are to be regarded as far more important than the thickness of the cytoplasm layer.

In *Salvinia* the rate of plasmolysis in a KNO_3 solution (HUBER and HÖFLER, 1930) proved to be 6 times as slow as in *Allium*, where mixtures of NaCl and $CaCl_2$ were used as plasmolyte (LEVITT *et al.*, 1936), whereas the rate of exosmosis in the latter is 20 times as slow as that observed in *Nitella* (KAMIYA and TAZAWA, 1956). These differences may partly be due to differences in the composition of the plasmolyte, but at any rate, in view of the doubtless not very important differences in the diameter of the cytoplasm layer, they seem to indicate that the main cause is to be sought in differences in the specific structure of the protoplasm. With regard to the high rate of exosmosis found by Kamiya and Tazawa, it is worth noting that the action of plasmolytes, no matter whether they are applied to ordinary cells or to artificially isolated gymnoplasts, is to be regarded as far more drastic than the treatment to which the *Nitella* cells in the experiments of Kamiya and Tazawa were exposed.

With regard to the behaviour of the protoplasts during plasmolysis it deserves our attention that they remain for some time attached to the cell wall by means of threads. GARDINER (1882) and BOWEN (1883) point out that at the moment the thread breaks one part of it withdraws towards the cell wall, whereas the rest withdraws into the protoplast. That not the whole thread is withdrawn into the protoplast, is perhaps not so astounding, as cell wall and protoplast are, at least in young cells, intimately connected; this was shown by BLANK and FREY-WYSSLING (1941) for the cells of *Zea mays* coleoptiles. In young cells the cell wall appears to contain a larger amount of protoplasm than in mature cells.

Similar threads may be drawn from the protoplasts by touching the latter with a needle. This is due to a change which the surface of the protoplast at this point undergoes; it obtains here a more strongly pronounced gel character and may even partially coagulate, as was noticed by CHAMBERS (1917), SEIFRIZ (1921) and SCARTH (1941). Just as in the investigations of PLOWE (1931), here too it was seen that these threads may contain clearly protruding globose swellings. Even if these threads do not break, it seems hardly probable that its constituent parts would return to their former position. Such lesions will cause a partial regeneration of the plasma-membrane, the structure of which in some places may differ strongly from the original one, and in this way differences in permeability and in elasticity may arise. Local differences in elasticity lead in gymnoplasts to deviations from the spherical shape.

Sometimes small swellings appear on the surface of the gymnoplast, and this usually leads to the expulsion of small globules of protoplasm, a process which begins slowly to lead subsequently to an abrupt diminution of the diameter of the gymnoplast.

The loss of fluidity and the kind of solidification dealt with in the preceding sections may also explain why in objects studied under the phase-contrast microscope no streaming motion of the protoplasm was found, whereas the latter was observed in the experiments of KONINGSBERGER (1947, b). YOTSUYANAGI (1953) too mentions that in his experiments the motion of the protoplasm came to a halt.

When plasmolysis and deplasmolysis proceed in a normal way, this may, according to PFEFFER (1877) and DE VRIES (1877), be regarded as a sign that the gymnoplasts are living and that they are not too badly damaged. That deplasmolysis in our experiments proceeded in a normal way, can be seen in our deplasmolysis graph, fig. 6, which shows the form that is characteristic for a diffusion process.

In order that this diffusion may take place, a selectively permeable plasma-membrane is a necessary condition, and the latter remains intact only so long as the cell is living. OSTERHOUT (1919) expresses this in the following way: permeability is "a delicate and accurate index of the vitality of the protoplasm" and "agents which produce injury increase permeability. The amount of increase may be regarded as a measure of the amount of injury". This is well illustrated by the very rapid deplasmolysis that we observe in isolated tonoplasts. This proceeds so vigorously that they explode long before the state of equilibrium is reached.

CHAPTER III

Experimental Part

§ 1. INFLUENCE OF THE TIME THE TISSUE SLICES REMAIN IN THE PLASMOLYTE ON THE RATE OF DEPLASMOLYSIS OF THE GYMNOPLASTS

In August 1954 we took some experiments in order to find out whether the time during which the tissue slices are kept in the plasmolyte might exercise an influence on the rate at which in the experiments proper the deplasmolysis proceeds. We wanted to know how long we might leave the slices in the plasmolyte without running the risk that the gymnoplasts become less suitable for our experiments. The plasmolyte we used in this case contained 0.66 mol dextrose, 0.04 n KNO_3 and 0.09 n $CaCl_2$. The Ca-concentration was rather high, as it was found that in the beginning of the season the gymnoplasts often burst when the plasmolyte contains less Ca. The firmness of the membrane was apparently increased by the presence of a larger amount of Ca-ions. After staying for 1 to 22 hours in thi plasmolyte, the gymnoplasts were isolated in a solution containing besides 0.66 mol dextrose and 0.04 n KNO_3 0.045 n $CaCl_2$. They were left in a watch-glass filled with this solution for about an hour in order that they might adapt themselves to the lower Ca concentration, and then transferred to the experimental vessel, which contained 1.6 ml of the same solution. Deplasmolysis was obtained by adding 0.6 ml aqua dest. The results are given in Fig. 9, where the h.v.c. expressed in minutes is set out against the time the tissue slices remained in the plasmolyte in hours.

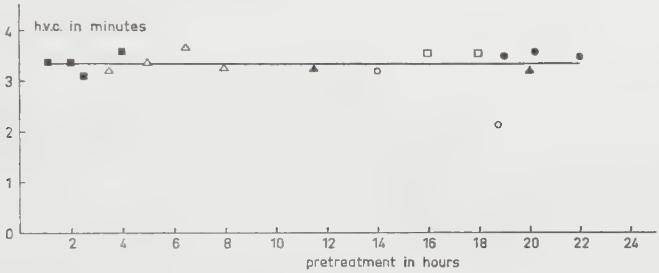

Fig. 9. Influence of the time during which the tissue slices remained in the plasmolyte on the magnitude of the h.v.c. Observations made on gymnoplasts obtained from the same onion are represented by the same sign. The experimental vessel contained 1.6 ml of a solution consisting of 0.66 mol dextrose, 0.04 n KNO_3 and 0.045 n $CaCl_2$. Deplasmolysis was obtained by adding 0.6 ml aq. dest. Temp. 24° C. Time: August 1954.

The time during which the slices stay in the plasmolyte appears on the whole to exercise little influence on the results of the experiments. Only when they remained longer than 18 hours in it, there is, as we see, an increase in variability. It is therefore allowed to use for experiments taken at different moments of the same day tissue slices that have been plasmolysed all at the same time. However, as a rule we did not leave them in the plasmolyte for more than 8 hours.

If the solution does not contain $CaCl_2$, the tissue slices can not be kept so long in it, as the gymnoplasts in that case prove to be less resistent and less firm.

The fact that the time the gymnoplasts stay in the plasmolyte, practically does not influence the h.v.c. indicates that the solutes of the plasmolyte do not affect the permeability of the protoplasmic layer. It seems justified to conclude that the solutes do not enter the protoplasm, otherwise the structure of the latter would have been altered.

In Fig. 9 we have indicated by the use of different signs that the gymnoplasts in the various series of experiments were obtained from different onions. The differences in the permeability for water shown by the gymnoplasts of different origin, prove to be rather small. Therefore, it is permissible to use in the same series of experiments gymnoplasts obtained from more than one onion.

§ 2. INFLUENCE OF TEMPERATURE ON THE PERMEATION RATE OF WATER

As it is always desirable to know in which way a physiological process depends upon temperature, we have studied the influence of the latter by comparing the results of experiments taken at 2° C, 9° C, 16° C, 24° C and 34° C. These experiments were taken in August and September 1954 and in January and February 1955.

Whereas in the preceding experiments besides $CaCl_2$, KNO_3 was added to the plasmolyte, we used here instead of KNO_3, KCl. This had the advantage that now only one kind of anions was present in the solution. The plasmolyte now contained 0.66 mol dextrose, 0.04 n KCl and 0.09 n $CaCl_2$. The gymnoplasts were, as soon as they had been isolated, transferred to the fluid that was to be used in the experimental vessel and which contained besides 0.66 mol dextrose 0.04 n KCl and 0.045 n $CaCl_2$. In case the experiments were to be performed either at 2° C, 9° C or 16° C, the gymnoplasts were given one hour to adapt themselves to these temperatures.

A temperature of circ. 2° C could be obtained by successively introducing small blocks of ice into the thermostat, and by passing water from the supply system through a copper spiral immersed in a refrigerant mixture of ice and common salt and then through a second copper spiral immersed in the thermostat. Especially in the experiments made at a temperature of 2° C, but also, though to a less degree, in those made at 9° C water tended to condense on the protuding part of the experimental vessel, and in order to prevent this, air was blown along the latter.

The experimental vessel contained 1.6 ml of a solution of 0.66 mol dextrose, 0.04 n KCl and 0.045 n $CaCl_2$, to which in order to obtain deplasmolysis 0.6 ml aq. dest. was added. When the experiments were made either at a very low or at a very high temperature, this caused a slight fluctuation of the temperature in the experimental vessel, as this water had room temperature (circ. 19° C).

At a temperature of 2° C it took the gymnoplasts at least an hour to reach the state of equilibrium, and so long, therefore, the experiments had to be continued; at a temperature of 9° C this took more than 45 minutes, at 16° C circ. 35 minutes, whereas at 24° C and at 34° C this state was reached in less than 30 minutes.

The results of these experiments are shown in Fig. 10*a*, where the h.v.c. has been plotted against the temperature.

In January and February 1955 another set of temperature experiments was made, viz. at 16° C, 24° C and 36.2° C, in order to study the effect of temperature on the volume of the protoplasts, to which we will return in section 4 of this chapter. The solution now contained besides 0.66 mol dextrose 0.09 n KCl and 0.04 n $CaCl_2$. The results of this set of experiments are shown in Fig. 10*b*.

To the influence of temperature on the permeability for water comparatively little attention has been paid, although the study of this problem started already with KRABBE (1896), who investigated the influence of higher temperatures and found it quite considerable. He pointed out that the osmotic temperature-coefficient was unable to account for the very marked increase in permeability found at the higher temperatures.

Fig. 10*a* and 10*b* show that between 2° C and 24° C the permeation increases at a higher rate than at higher temperatures, as KRABBE (1896) and VAN RIJSSELBERGHE (1902) already had noticed. As the effect of temperature on the speed of a reaction is best judged by comparing the values calculated for Q_{10}, we decided to use the data given in Fig. 10*a* and 10*b* for calculating this coefficient for the rate of deplasmolysis at successive temperature intervals. To this end we had to take the reciprocal values of the h.v.c., as the rate of deplasmolysis is inversely proportional to the latter. The values calculated for Q_{10} are given in Table VI.

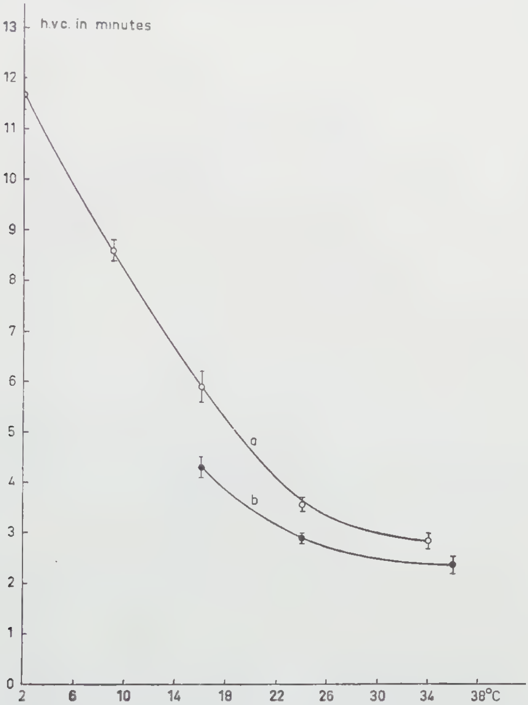

Fig. 10. Influence of temperature on the h.v.c. The solution in the experimental vessel contained in the experiments of which the results are shown in *a*. 0.66 mol dextrose, 0.04 n KCl and 0.045 n $CaCl_2$ and in the experiments of which the results are given in *b*. 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$. In both sets of experiments the experimental vessel contained 1.6 ml solution, and for diluting this solution in both sets 0.6 ml aq. dest. was used.

In Table VI*a* Q_{10} increases up to 24° C but at still higher temperatures it decreases. This is less apparent in Table VI*b*, although here also Q_{10} is decreasing.

TABLE VI

Increase, expressed by means of Q_{10}, of the speed with which deplasmolysis proceeds with increase of temperature

a. solution in the experimental vessel containing 0.66 mol dextrose, 0.04 n KCl and 0.045 n $CaCl_2$	*b.* solution in the experimental vessel containing 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$
$Q_{4-14} = 1.66$ $Q_{14-24} = 1.88$ $Q_{24-34} = 1.38$	$Q_{16-26} = 1.90$ $Q_{26-36} = 1.70$

In chapter IV we will try to find an explanation for the decrease in the value of Q_{10}, but with regard to the difference between the corresponding values of this coefficient given in Table VI*a* and *b*, we wish to draw the attention to two factors that might be involved. They are (1) a seasonal difference, and (2) a difference in the amount of KCl in the experimental solution. An influence of the latter factor was already noted by BELEHRADEK (1935), who, however, did not give an explanation of the way in which it might act.

Because of the decrease in the Q_{10} above 24° C the latter temperature was chosen for the rest of our experiments. A further advantage of this temperature is that fluctuations of the latter will affect the permeation rate but slightly (cf. Fig. 10). A disadvantage is that changes in the permeation rate will be smaller and therefore less easily observable than e.g. at 16° C, where the slope of the graph in which these changes are recorded is steeper.

§ 3. EFFECT OF THE MANNER IN WHICH THE SOLUTION IN THE EXPERIMENTAL VESSEL IS DILUTED ON THE PERMEABILITY FOR WATER

As we intend to investigate changes in the rate at which deplasmolysis proceeds, i.e. in the rate at which water permeates the protoplasm, it is of importance to know whether the manner in which the solution in the experimental vessel is diluted, has any effect on this rate.

To solve this question we have diluted this solution, which in this case contained 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$, in two ways. In one set of experiments the solution was diluted as a whole, which meant that the concentration of the dextrose and that of the ions decreased in the same way, whereas in the second set the concentration of the ions was kept constant. All these experiments were taken in November and December 1954.

The results are shown in Fig. 11, where the values determined for the h.v.c. in a large number of gymnoplasts are set out against the concentration, expressed in atmospheres, of the diluted solution. The dilution was obtained either with various amounts of aq. dest. or with a solution of KCl and $CaCl_2$ in the same concentration as in the undiluted solution. The osmotic value of the latter was 20.8 atm.

As the endosmosis of water depends in the first place upon the difference in concentration inside and outside the gymnoplast and not upon the nature of the solutes, the concentration is best expressed in atmospheres. The osmotic value of the dextrose concentrations has been calculated by the aid of the tables given by LANDOLT-BÖRNSTEIN (1923) and by the ROY. NETH. CHEM. SOC. (1952). The figures given in these tables have been based on the specific weight of dextrose, and this was derived from that of saccharose. To calculate the osmotic values of the KCl and $CaCl_2$ concentration the activity coefficients had to be taken into account; the latter too were taken from the work of Landolt-Börnstein [1]).

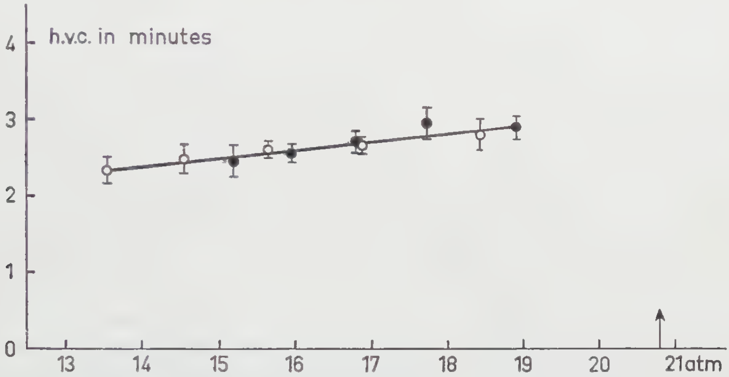

Fig. 11. Effect of the change in concentration expressed in atmospheres on the value of the h.v.c. expressed in minutes. The undiluted solution contained 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$; it is indicated by the sign ↑. The results of the experiments in which the solution was diluted in such a way that the concentration of the ions remained the same, are indicated by the sign ●; the results of those in which the solution was diluted with aq. dest. by the sign ○.
Temp. 24° C. Time: November and December 1954.

It has been found that the activity coefficient of a mixture of salts is not equal to the sum of the activity coefficients of the component parts, and it is therefore not impossible that experimental determination of the osmotic value of our solutions would have given values that differed from those we calculated. Moreover, according to KAHO (1956), mono- as well as disaccharides and various salts would exercise an antagonistic action on each other; however, it should be borne in mind that he worked with rather high salt concentrations.

The most suitable composition of the plasmolyte was here also experimentally determined. The effect of the season shows itself clearly in the concentration of KCl and of $CaCl_2$ that were required to give the plasma-membrane the necessary degree of firmness. They proved to be markedly smaller than in the period during which the experiments on the effect of temperature were made.

The behaviour of the protoplasts in the experiments in which the two modes of diluting were compared, was on the whole not markedly different. In the more strongly diluted solutions, however, a larger number of exploding gymnoplasts were noted.

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[1]) For advice concerning the calculation of the osmotic values I am greatly indebted to Dr A. F. Peerdeman and to Dr H. Reerink.

The answer to the question whether there is a marked difference between the results obtained with the two modes of diluting, is also of importance because it is at the same time an answer to the question whether diluting with pure water, i.e. diminution of the ion concentration, must be regarded as harmful to the cell. HEILBRUNN (1928) already pointed out that in order to obtain comparable results with regard to the effect of various salts on the protoplasm, we have to work with isotonic solutions. In our experiments it is not enough that the undiluted solutions are isotonic, but we should also pay attention to the concentration of the diluted solution. After diluting with pure water, the osmotic value of the solution is lower than after diluting with a solution containing 0.09 n KCl and 0.04 n $CaCl_2$. However, as we may see in Fig. 11, no qualitative differences were observed.

We need not be afraid, therefore, that diluting with pure water will have a harmful effect, e.g. by withdrawing ions, provided there is a sufficient amount of salts in the solution. However, when we use as plasmolyte a solution of dextrose without any salts, the situation is apparently quite different, for then the gymnoplasts are seen to loose their spherical shape, which means, as we have already pointed out in Chapter II § 2, that the protoplasm has lost part of its consistency. For this reason the belief that in experiments on plasmolysis a previous immersion in water would be entirely harmless, as since the days of DE VRIES (1877) and PFEFFER (1877) has generally been accepted, does not seem to be fully justified. It would at any rate be necessary to take controll experiments. Whether the immersion in water will be harmful or not, will depend upon the proportion between the amount of Ca-ions that pass into the water and the amount that will be retained in the plasma-membrane. The investigations of WINKLER and BUNGENBERG DE JONG (1940/41) have shown that the concentration of the Ca-ions in the plasma-membrane of erythrocytes may become so small that the presence of the latter can no longer be demonstrated. ALBACH (1931) points out that the plasma-membrane in the cells of *Rhoeo discolor* regains its original firmness when the cells are transferred from pure water to tap water, the small amount of salts that are dissolved in the latter being sufficient to this end.

§ 4. THE CHANGES THE VOLUME OF THE GYMNOPLAST UNDERGOES DURING PLASMOLYSIS AND DEPLASMOLYSIS

As in our experiments the permeation of water is caused by the changes of the osmotic value that were brought about in the fluid in which the gymnoplasts were immersed, we will have to see within what limits the laws of osmosis may here be applied. Three questions present themselves to us, viz. *A.* in how far may the gymnoplasts be regarded as ideal osmometers to which van 't Hoff's law of osmosis is applicable, *B.* how do they comport themselves at various temperatures, and *C.* what effect has the proportion of the concentrations in which the various salts are present in the plasmolyte.

A. Van 't Hoff's law, $\pi . V = C$

The slices of onion tissue were plasmolysed in a solution containing 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$, and the experimental vessel at the start was filled with a solution of the same composition. The temperature in the thermostat was 24° C. Deplasmolysis was obtained by adding a salt solution in which KCl and $CaCl_2$ were present in the same concentration as in the plasmolyte. After that, the gymnoplasts were plasmolysed once more by adding a solution containing 2 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$. Subsequently the concentration of the solution in the experimental vessel was alternately decreased or increased by addition either of the salt solution or of the plasmolysing solution. Now, in order to find out whether van 't Hoff's law was fully applicable, we merely had to compare the values found for the diameter of the gymnoplast expressed as a percentage of the original diameter and raised to the third power, as it is the relative increase of the volume that matters. In Fig. 12 these relative values found for the increase in volume of the gymnoplasts are set out against the changes in the concentration of the solution expressed in atmospheres. An arrow directed upwards (↑) indicates a change caused by a decrease of the concentration, an arrow directed downwards (↓) one that is due to an increase. As each gymnoplast underwent several changes in volume, the latter have been numbered, and the number put down next to the arrow. The curve gives the values of the relative changes in volume calculated by the aid of van 't Hoff's formula.

TABLE VII

The osmotic values of the usually applied plasmolytes; temp. 24° C.

dextrose	KCl	$CaCl_2$	Atm.	dextrose	KCl	$CaCl_2$	Atm.
0.66 mol	0.04 n	0.045 n	18.85	0.66 mol	0.10 n	—	19.95
	0.09	0.04	20.80		0.09	0.01 n	19.85
	0.09	0.01	19.85		0.07	0.03	19.60
	0.02	0.09	19.28		0.05	0.05	19.33
	0.08	0.09	21.98		0.03	0.07	19.08
	0.18	0.02	24.25		0.01	0.09	18.82
	—	—	—		—	0.10	18.64

Deplasmolysis appeared to proceed in a fairly regular way, but this cannot be said of plasmolysis. During the initial stages of the latter the gymnoplasts assume rather capricious shapes, which remind one of the "schäumige Degeneration" described by KÜSTER (1929) and of the frothy structures obtained by BUNGENBERG DE JONG (1932)

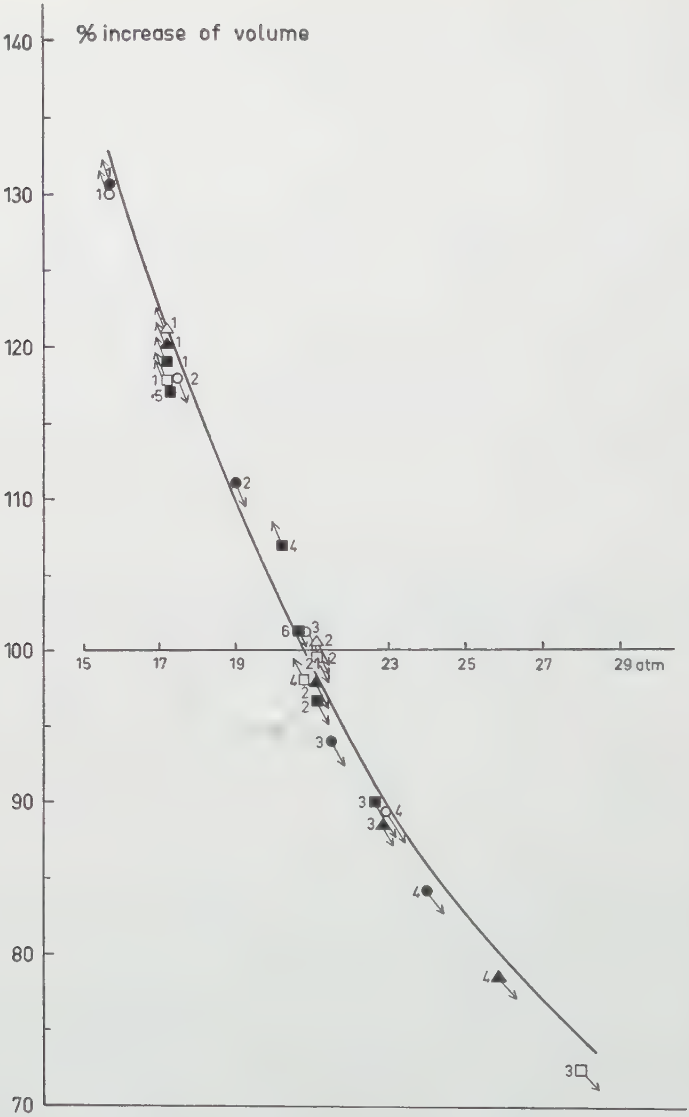

Fig. 12. Effect exercised by a change in the osmotic value of the solution in the experimental vessel on the volume of the gymnoplasts. The solution in the experimental vessel originally contained 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$. The changes in its osmotic value were brought about by adding either solution *a*, containing 0.09 n KCl and 0.04 n $CaCl_2$ only, or solution *b*, containing 2 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$. An arrow directed upwards (↑) indicates a change in volume caused by a decrease of the concentration, an arrow directed downwards (↓) one caused by an increase. The number of the change is indicated by means of the figure next to the arrow. Temp. 24° C. Time: November 1954.

in mixtures of various hydrophilic colloids. The cause of these irregularities may perhaps be found in the peculiar way in which the dextrose solution, which has a much higher viscosity than the diluted solution, mixed with the latter. The molecules of the more viscous fluid are not at once regularly dispersed through the less viscous one, but cohere in the form of slimy cords which wind their way through the other fluid and also, of course, along the gymnoplasts. The latter therefore are at various points of their surface in contact with fluid of a very different composition and osmotic value, and this might well lead to strong deformations. Because of the high degree of elasticity of the protoplasm the gymnoplasts will tend, as PLOWE (1931), SEIFRIZ and PLOWE (1931) and SEIFRIZ (1952) suppose, to regain their spherical shape. This requires circ. 20 minutes. The undesirable effect of this way of mixing could, to some extent, be diminished in the following manner. Part of the solution in the experimental vessel was sucked into the receptacle that forms part of the tube (g), Fig. 2, and in the latter mixed with the other fluid; after the mixing was completed, this mixture, whose viscosity does not differ so strongly from that of the fluid in the experimental vessel, was added to the rest of the latter.

For the reason explained in the preceding section we had to confine our attention to the volume in the state of equilibrium. If the gymnoplasts would behave as ideal osmometers, the formula $\pi . V = C$ would be applicable to them, and the measured values would all find their place on the theoretical curve. However, this is not so. After the fluid in the experimental vessel had been diluted for the first time, the volume of the gymnoplasts appeared to remain below the expected value, and after the second plasmolysis we found it, on the contrary, occasionally larger than the theoretical value. It is not impossible that the last-named deviation from the expected result may be due to the drastic changes that take place during the second plasmolysis. The protoplasm may on account of them have grown more rigid, so that the volume pertaining to the state of equilibrium cannot be reached. It should be noted that the reliability of the results decreases with each successive change, as at each time some of the gymnoplasts have to be eliminated; after the sixth change only two of them were left.

B. Van 't Hoff–Mariotte's law, $\pi V = RT$

We have also tried to find out whether the combined effect of osmotic value and temperature on the volume of the gymnoplasts obeys the law of van 't Hoff–Mariotte. To this end we could use the data obtained in our experiments on the effect of temperature on the rate at which water passes the plasma-membrane, i.e. the experiments dealt with in section 2 of this chapter. All we had to do was to calculate the final volume.

As mentioned in § 2 the temperatures at which the experiments were taken, were 2° C, 9° C, 16° C, 24° C and 34° C. The plasmolyte contained 0.66 mol. dextrose, 0.04 n KCl and 0.09 n $CaCl_2$; the solution in the experimental vessel, however, contained instead of 0.09 n $CaCl_2$ only 0.045 n $CaCl_2$. This solution was made at room temperature, which in the experiments taken at a different temperature caused a slight error in the calculation of the osmotic value. The 1.6 ml solution in the experimental vessel was diluted by adding 0.6 ml aq. dest.

The difference between the osmotic values at 34° C and at 2° C amounted to 2 atmospheres, and the decrease of the osmotic value was at 34° C 5.2 atm. and at 2° C 4.6 atm.; in the other experiments it lays between these two values. The relation between temperature and gymnoplast volume at an approximately constant decrease in the osmotic value is shown in Fig. 13. The experiments described above were taken in August and September 1954, and their results are given in this figure under *a*.

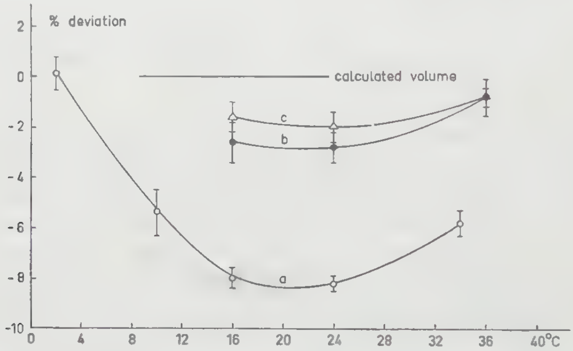

Fig. 13. Effect of temperature upon gymnoplast volume at an approximately equal decrease of the osmotic value. The Y-axis gives the difference between the theoretical and the actually observed gymnoplast volume expressed as a percentage of the initial volume. The composition of the 1.6 ml solution in the experimental vessel differed in the three sets of experiments; in *a* it was 0.66 mol dextrose, 0.04 n KCl and 0.045 $CaCl_2$, in *b* and *c* 0.66 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$. In *a* and *b* the solution was diluted by adding 0.6 ml aq. dest., in *c* by adding 0.6 ml of a solution containing KCl and $CaCl_2$ in the same concentration as in the solution in the experimental vessel. Time: *a* August and September 1954, *b* and *c* January and February 1955.

In Fig. 13*a* the relation between temperature and the difference between the values that were calculated and those that were actually observed appears to be of a peculiar nature. This aberrant behaviour might be explained in three different ways. It might be due (1) to the difference in composition between the plasmolyte and the undiluted solution in the experimental vessel, (2) to the use of distilled water for diluting this solution, and (3) to a seasonal influence. To test these possibilities we took in January and February 1955 two other sets of experiments, of which the results are shown in Fig. 13*b* and *c*. In these experiments the composition of the plasmolyte and the undiluted solution in the experimental vessel was the same. The latter was in set *b* diluted with distilled water and in set *c* with a solution of 0.09 n KCl and 0.04 n $CaCl_2$. As it is technically rather difficult to work at 2° C and 9° C, we confined ourselves in these experiments to 16° C, 24° C and 36° C. Moreover, as there are no differences of a qualitative nature between the results obtained in the experiments at the lower temperatures and those taken at the higher ones, it did not seem necessary to repeat all of them.

That the volume found in the experiments of set *b* would deviate slightly more from the theoretical value than that found in set *c*, would be no wonder, as the deplasmolysing solution used in set *b* is somewhat weaker. It is, however, not quite certain that the difference we actually observed may be regarded as significant. It seems at any rate clear that the way in which the diluting is carried out, is of no importance. The larger deviation from the theoretical value observed in the experiments of set *a* can therefore not be due to the second of the possible causes mentioned above, viz. to a difference in the osmotic value of the deplasmolysing solution, as the deviation is too large. As we have already pointed out in section 2 of this chapter, it may be due either to the difference in the proportion in which the ions are represented in the deplasmolysing solution or else to a seasonal influence, i.e. to one of the possibilities mentioned under 1 and 3.

C. *Comparison between the gymnoplast volume observed in solutions in which the proportion between the concentrations of the various salts differs, with that calculated on the base of van 't Hoff's law*

The first of the two possibilities mentioned in the last sentence of the preceding section was tested in a series of experiments in which the solution in the experimental vessel differed in composition and was diluted in different ways. These experiments were performed at a temperature of 24° C. The experimental vessel originally contained 1 ml solution, and the amount of fluid used for diluting the latter was in the first two sets of experiments 0.2 ml and in the third set 0.4 ml.

The solution in the experimental vessel originally contained 0.66 mol dextrose and various amounts of KCl and $CaCl_2$; the sum of their concentrations, however, was always 0.1 n. These solutions were diluted by adding either distilled water or a salt solution consisting of KCl and $CaCl_2$ in the same proportion and in the same concentration as in the undiluted fluid. The volume of the gymnoplasts was determined in the same way as above. The results are represented in Fig. 14.

The graphs which show the results of the sets *a* and *b* are on the whole similar. The difference between the calculated value and the observed one proves to be maximal when the solution contained 0.05 n KCl and 0.05 n $CaCl_2$, and minimal when only one of the salts was present. The variability proved to be largest when the solution contained KCl only, viz. ± 0.38 in set *a* and ± 0.41 in set *b*.

It is not impossible that this KCl concentration may have had a harmful effect on the form of the gymnoplasts, as we have already pointed out in Chapter II, § 2. This would explain why the difference between the observed and the calculated value of the volume is higher in set *a* than in set *b*, whereas the K-concentration is higher in set *b* than in set *a*. In set *b* the tendency to a smaller difference between the calculated value and the observed one with increasing Ca-concentration appeared to be stronger too.

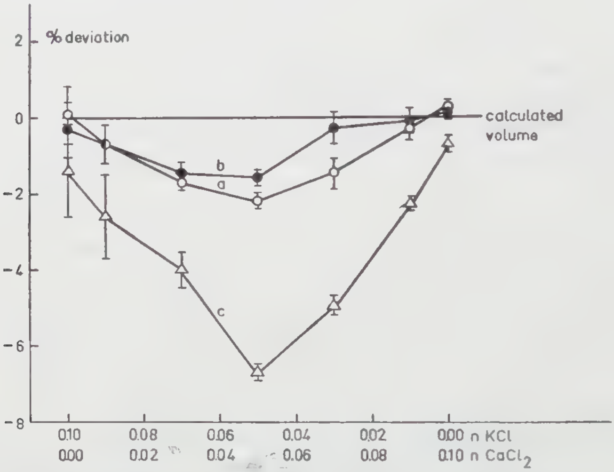

Fig. 14. Relation between the proportion of KCl and $CaCl_2$ in the solution and the difference between the calculated and the observed value of the gymnoplast volume. The 1.0 ml solution in the experimental vessel originally contained 0.66 mol dextrose, and KCl and $CaCl_2$ in the proportion indicated in the figure. It was diluted in set *a* by adding 0.2 ml aq. dest., in set *b* by adding 0.2 ml of a salt solution containing KCl and $CaCl_2$ in the same concentration as they have in the undiluted solution, and in set *c* by adding 0.4 ml aq. dest. Temp. 24° C. Time: for *a* and *b* February and March 1955; for *c* January 1956.

Because of the high values found for the difference between the calculated and the observed effect of the osmotic value, it seemed desirable to repeat these experiments. This was done in January 1956. This time we decided to go somewhat further with the dilution in order to obtain, if possible, a stronger effect. We diluted therefore with distilled water and with double the amount we had used in set *a*. The results of these experiments are shown in graph *c* (Fig. 14). Qualitatively they are the same as in the sets *a* and *b*, but the differences are indeed larger.

The results of these three sets of experiments doubtless permit us to conclude that the gymnoplast does not behave under all circumstances as an ideal osmometer. However, it might be possible to choose the circumstances in such a way that for some time they would indeed act as such. This dependence upon a definite set of circumstances might be one of the reasons why in the literature so strongly deviating results have been recorded. The difference between the observed value of the gymnoplast volume and that which it would have when the laws of van 't Hoff were unconditionally applicable, must be due to changes in the structure of the protoplasm, and here we think in the first place of the latter's structurally determined viscosity and elasticity and the way in which these apparently is influenced by temperature and by the proportion between the concentrations of the various ions in the fluid in which the gymnoplast is immersed. In chapter IV we will return to this question.

§ 5. THE EFFECT EXERCISED BY THE CONCENTRATION OF DEXTROSE AND OF THE K- AND CA-SALTS IN THE SOLUTION ON THE PERMEATION RATE OF WATER

In order to be in a better position to judge the results of the experiments described in § 3 of this chapter, it seemed desirable to repeat them with a solution in which the K- and Ca-concentration was the same, but in which the dextrose concentration had been changed. We experimented, therefore, with a plasmolyte containing 1.16 mol dextrose, 0.09 n KCl and 0.04 n $CaCl_2$; by adding 0.3 ml distilled water to 1 ml of this solution in the experimental vessel we brought the concentration of the dextrose down to 0.89 mol.

As value for the h.v.c. we now found 2.27 ± 0.15 min., whereas in the solution containing 0.66 mol dextrose used in the experiments of section 3 for the same decrease in osmotic value, *viz.* 6.3 atm. the h.v.c., as may be concluded from Fig. 11, is 2.42 min. The difference between the two values found for the h.v.c. is negligible, and it seems therefore safe to conclude that the difference between the two concentrations is not large enough to cause a marked change in the structure of the protoplasm. The more concentrated dextrose solution will merely exercise a somewhat more strongly dehydrating action.

It is equally desirable to know how the permeation rate is influenced by the proportion between the concentration of the K- and Ca-salts when the dextrose concentration remains the same. To determine this relation we kept the concentration of one of the salts constant and varied that of the other and vice-versa. We also varied the concentration of both salts, but in that case the proportion was kept constant. Deplasmolysis was obtained by adding 0.2 ml distilled water to the 1 ml solution in the experimental vessel. The composition of this solution is given in the second main column of Table VIII. The experiments were made in December 1954 and in January 1955.

In studying the influence exercised by the total concentration and by the proportion between the K- and Ca-concentrations, we will first of all have to eliminate the difference in the osmotic values of the solutions. To this end we compared *a.* the results of the sets 1 and 2, *b.* those of the sets 3 and 4, and *c.* those of the sets 2 and 5 (cf. Table VIII).

In set 1 the decrease of the osmotic value on account of the dilution is 0.25 atm. larger than in set 2, whereas the h.v.c. is in set 1 0.22 min. larger than in set 2, which is circ. five times as much as we would

Table VIII

Relation between the total salt concentration and the proportion between the K- and Ca-concentration on the one hand and the permeation rate of water on the other. The original composition of the solution in the experimental vessel is given in the second main column. Deplasmolysis was obtained by adding 0.2 ml aq. dest. to the 1 ml undiluted solution. Temp. 24° C. Time: December 1954 and January 1955.

Set	Initial concentrations			Osmotic value in atm.			the h.v.c. in min.
	dextrose	KCl	$CaCl_2$	undiluted	diluted	difference	
1	0.66 mol	0.09 n	0.04 n	20.80	17.33	3.57	2.68 ± 0.12
2	id.	0.09 n	0.01 n	19.85	16.53	3.32	2.46 ± 0.14
3	id.	0.02 n	0.09 n	19.28	16.10	3.18	3.56 ± 0.09
4	id.	0.08 n	0.09 n	21.98	18.35	3.63	2.28 ± 0.13
5	id.	0.18 n	0.02 n	24.25	20.23	4.03	2.30 ± 0.10

have found when we had calculated the h.v.c. by the aid of the data shown in Fig. 11 under the assumption that the effect depends on the decrease in concentration alone. The actually present, much larger difference between the h.v.c. values must therefore be ascribed to the difference in the proportion between the K- and Ca-concentrations. Here it must be the higher Ca concentration, which has changed the structure of the plasma-membrane.

In set 3 the decrease of the osmotic value on account of the dilution is 0.45 atm. less than in set 4, whereas the h.v.c. is in set 3 1.22 min. larger than in set 4. Here too the high value of the difference in the h.v.c. is to be ascribed to the difference in the proportion between the K- and Ca-concentrations, in this case therefore to the larger K-concentration. The latter too will therefore have changed the structure of the plasmamembrane.

Above we came to the conclusion that the way in which the deplasmolysis proceeds, depends to a large extent upon the proportion between the concentration of the K-and Ca-salts, and if this is correct, we will have to expect that the difference in the value for the h.v.c. found in the sets 2 and 5 will be conform to the difference in the decrease of the osmotic value. This amounts to 0.71 atm., and if we calculate the difference between the corresponding values for the h.v.c. that would have to be expected on account of this figure, we see that it comes very near to the value that we actually found. The slight deviation from the calculated value might perhaps be ascribed to the larger concentration of the K-salt in set 5. An influence of the latter is already noticeable during plasmolysis, for the gymnoplasts of set 5 assume the spherical shape in a much shorter time, and they become, moreover, more or less glassy.

On account of the results of these experiments we may therefore conclude that a change in the proportion of the concentrations in which the K- and Ca-salts are present, has a much larger effect on the structure of the protoplasm than a change in the total salt concentration would have when the latter was not accompanied by a change in the proportion of the constituent salts.

§ 6. Effect of the proportion between the K- and Ca-concentration on the permeation rate of water

The experiments described in the preceding section have shown that the permeation rate of water is influenced by the proportion between the K- and the Ca-concentration in the solution in which the gymnoplasts are immersed. We will now enter somewhat deeper into this relation, using to this end the results of experiments taken in February and March 1955. The initial concentration of the dextrose was in these experiments always the same, viz. 0.66 mol, whereas the concentrations of KCl and of $CaCl_2$ varied, but so that the sum of the concentrations expressed as a fraction of n always remained the same, viz. 0.1. Of this solution 1 ml was poured into the experimental vessel, where it was diluted by adding in the first set of experiments (Fig. 15*a*) 0.2 ml distilled water and in the second (Fig. 15*b*) 0.2 ml of a salt solution containing KCl and $CaCl_2$ in the same concentration as in the undiluted solution; in the experiments of set *b* it was therefore the dextrose concentration alone that underwent a decrease.

The results are shown in the form of graphs (Fig. 15) in which the proportion between the KCl and the $CaCl_2$ concentration are set out against the h.v.c. expressed in minutes.

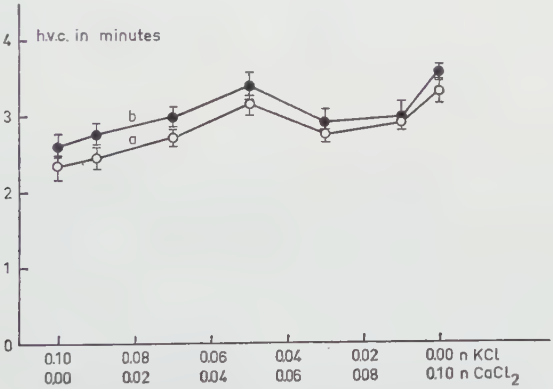

Fig. 15. Effect of the proportion between the KCl and the $CaCl_2$ concentration on the h.v.c. The solution in the experimental vessel contained besides 0.66 mol dextrose KCl and $CaCl_2$ in the concentrations that are indicated at the base of the figure. In set *a* the solution was diluted with aq. dest., in set *b* with a solution of KCl and $CaCl_2$ in the same proportion and in the same concentration as in the undiluted solution. The amount of the undiluted solution was 1 ml, that of the fluid used for diluting 0.2 ml. Temp. 24° C. Time: February and March 1955.

In the solution containing 0.1 n KCl plasmolysis proceeded rapidly, and so we could already begin after half an hour with the isolation of the gymnoplasts. The number of tonoplasts, on the other hand, appeared to be much larger than in the other solutions. It was therefore advisable to leave the tissue slices not too long in the plasmolyte. Plasmolysis in a solution containing 0.1 n $CaCl_2$, on the contrary, proceeded very slowly; here it took circ. 6 hours before the protoplasts had freed themselves from the cell wall and had assumed a spherical shape.

The very marked effect of the proportion between the K- and the Ca-concentration on the rate at which plasmolysis proceeds and on the time required for the isolation of the protoplasts, is in complete agreement with what has been said on this subject in Chapter II, § 1.

Especially in a solution without $CaCl_2$ we have to take care that the gymnoplasts do not touch each other. They not only require space for expansion during deplasmolysis, but at all stages fusion between them is possible, and this should be prevented. It is not necessary that the gymnoplasts are still connected with each other by means of plasma threads, for fusion also takes place between completely free ones. The tendency to fuse depends, as MISSBACH (1928) has shown, upon the composition of the solution, but, as we know from HOFMEISTER (1954) it may also be due to mechanical lesions. In the latter's experiments too the tendency to fuse was larger when the solution contained only dextrose and KCl than when $CaCl_2$ was also present. After having adduced arguments in favour of the view that the plasma-membrane does not only contain lipoids but also proteins, Hofmeister points out that the "junctions" between the latter in the various boundary layers might be loosened by the K-ions, and that in the points where the protoplasts are in contact with each other, these loosened parts of the proteins would enter into new connections, and so effect a fusion between the protoplasts. The Ca-ions would have an opposite effect.

These results are a welcome confirmation of the findings of WEBER (1921) and SEIFRIZ and PLOWE (1931), viz. that it is easier to draw threads from the surface of an isolated protoplast by touching the latter with a needle when the protoplasts are immersed in a solution of dextrose and KCl than when the solution contains $CaCl_2$ instead of KCl, although the few threads that can be obtained in the latter case prove to be firmer and can be drawn out to greater length before they break.

Before entering into a more thorough analysis of the influence exercised by the proportion in which the K- and Ca-salts are present, we will have to find out whether a difference in the way in which the solution is diluted and its osmotic value lowered, might be of importance. In the experiments in which the salt concentration remained the same and in which the decrease of the osmotic value therefore was only due to a decrease of the dextrose concentration (Fig. 15*b*) this factor evidently played no part. Such differences are confined to the experiments of set *a* (Fig. 15*a*), where the decrease of the osmotic value was brought about by a decrease in the concentration of all the constituent parts of the solution, i.e. by that of the salts as well as by that of the dextrose. Here the decrease of the osmotic value was maximal when the solution contained besides the 0.66 mol dextrose 0.09 n KCl and 0.01 n $CaCl_2$, viz. 3.32 atm., and minimal when besides the dextrose 0.01 n KCl and 0.09 n $CaCl_2$ was present, *viz.*

3.10 atm. The difference in the decrease of the osmotic value amounted therefore at the most to 0.22 atm. Differences of this order of magnitude are too small to be held responsible for the differences found in the h.v.c. value, and they certainly are also unable to explain the difference in shape of the graphs shown in Fig. 15, for if the latter depended on a difference of this kind, graph *a* should be a straight line and graph *b* could not possess such a pronounced top. The difference in osmotic value due to the dilution of the corresponding solutions used in set *a* and *b* amounts maximal to 0.77 atm., viz. when the solution contains 0.09 n KCl and 0.01 n $CaCl_2$, and is minimal 0.55 atm., viz. if the proportion between KCl and $CaCl_2$ is reversed. When we leave the degree of variability out of consideration, the difference between the results of the two sets appears to be rather small.

In the experiments of set *a* as well as in those of set *b* the value for the h.v.c. increases with the increase of the concentration of the Ca-salt and the decrease of that of the K-salt until the concentration of both salts has become 0.05 n, and as this increase in both sets is regular, the manner of diluting is obviously of no consequence. When the increase of the concentration of the Ca-salt and the decrease of that of the K-salt continue, the value for the h.v.c. begins to decrease to reach its lowest value when the solution contains besides the 0.66 mol dextrose 0.07 n $CaCl_2$ and 0.03 n KCl. After that it increases again.

In Chapter IV we will try to find an explanation for the form of these graphs.

§ 7. Effect of the chlorides of alkali metals and of alkaline earth metals on the rate of deplasmolysis in gymnoplasts

Up to know we have dealt only with the effect of the chlorides of K and Ca on the structure of the protoplasm as it manifests itself in the degree of permeability for water. However, we should also like to know what effect the chlorides of the other alkali metals and alkaline earth metals exercise on the degree of permeability for water in order to be in a better position for giving an explanation of the way in which the permeability of the protoplasm is affected by the cations of these salts.

In preliminary experiments we took to this end, deplasmolysis was obtained in the same way as in our previous experiments. The onion-tissue slices were immersed in plasmolytes of various composition. The latter always contained 0.66 mol dextrose but in addition in set *a* a 0.05 n solution of the chloride of one of the alkali metals plus 0.05 n $CaCl_2$, and in set *b* a 0.05 n solution of the chloride of one of the alkaline earth metals plus 0.05 n KCl. The undiluted solution in the experimental vessel had the same composition as the plasmolyte, and deplasmolysis was obtained by adding 0.2 ml water to 0.3 ml of the undiluted solution. The temperature in the thermostat was kept at 25° C, and the tissue slices were obtained from onions in the resting period (January and February 1956).

The results are given in Table IX, which enables us to compare the h.v.c. values with the composition of the plasmolyte.

TABLE IX

Influence of chlorides of alkali and alkaline earth metals on permeability for water. The experimental vessel contained 0.3 ml of a solution of 0.66 mol dextrose and in addition two salts together in a concentration of 0.1 n; in the first set of experiments one of the salts always was $CaCl_2$, the other one a chloride of an alkali metal, in the second set one always was KCl, the other one a chloride of an alkaline earth metal. Deplasmolysis was obtained by adding 0.2 ml aq. dest.

Temp. 25° C.			Time: January and February 1956
Combination of salts			the h.v.c. in minutes
a.	0.05 n RbCl	0.05 n $CaCl_2$	1.89 ± 0.18
	0.05 n LiCl	id.	2.00 ± 0.34
	0.05 n CsCl	id.	2.04 ± 0.25
	0.05 n NaCl	id.	2.20 ± 0.21
	0.05 n KCl	id.	2.48 ± 0.16
b.	0.05 n KCl	0.05 n $CaCl_2$	2.48 ± 0.16
	id.	0.05 n $SrCl_2$	2.34 ± 0.27
	id.	0.05 n $BaCl_2$	1.94 ± 0.36
	id.	0.05 n $MgCl_2$	no success
	id.	0.05 n $BeCl_2$	1.59 ± 0.47

As a rule no difficulties were experienced with plasmolysis and the isolation of the gymnoplasts so long as the plasmolyte did not contain LiCl, $MgCl_2$ or $BeCl_2$.

The divergent character of the influence exercised by LiCl manifested itself in the explosion of a large number of gymnoplasts during deplasmolysis and in the irregular shape they often assumed. The protoplasm, moreover, looked swollen. Only a small number of gymnoplasts (on the average 5, i.e. ca. 15 %) survived deplasmolysis.

Plasmolysis with a solution containing $MgCl_2$ was tried 30 times, but each time without success. Most of the gymnoplasts either exploded or fused.

An entirely different effect was obtained when the plasmolyte contained $BeCl_2$. About half the number of tissue slices assumed a yellowish green colour. At first they were colourless and looked normal, but in a few minutes they turned yellowish-green. This colour change presumably indicates a chemical reaction of the Be-ions either with a constituent of the protoplasm or with the contents of the vacuole. This supposition finds support in the fact that the colour change appears immediately when the tissue slices are crushed in the $BeCl_2$ solution.

As it seemed possible that the change in colour might be due to hydrolysis of $BeCl_2$, the tissue slices were crushed in solutions of hydrochloric acid or of acetic acid with a pH varying from 3 to 6.5 It appeared that within this pH range no colour change took place.

and the change in colour in the $BeCl_2$ solution can therefore not be due to the decrease of the pH that would accompany the hydrolysis of that salt.

As a rule no gymnoplasts could be isolated from the tissue slices that showed the yellowish-green discoloration. The protoplasts were obviously damaged. Of those that could be set free, some turned yellowish-green during deplasmolysis, and these, as a rule, then exploded almost immediately. The few discoloured gymnoplasts that survived, showed a sudden increase of permeability and reached an unusually large size. At the end of the experiment only 3–7 still normally looking gymnoplasts (i.e. 10 to 23 % of the total number) were left.

The experiments taken with the solution containing KCl and $CaCl_2$ may be regarded as a link between those in which the solution besides $CaCl_2$ contained the chloride of one of the other alkali metals (set *a*) and those in which it contained besides KCl the chloride of one of the other alkaline earth metals (set *b*), and for this reason this experiment has been included in both sets. Table IX shows that the value calculated for the h.v.c. shows a fairly high degree of variability. In set *b* this variability is generally somewhat larger than in set *a*. It appears moreover that it increases with the distance that separates the various alkali metals in the periodic table from K and the various alkaline earth metals from Ca. In the experiment with RbCl and $CaCl_2$, however, the degree of variability differed but slightly from that found in the experiment with KCl and $CaCl_2$.

If we wish to compare the results due to the action of the various salt solutions on the protoplasm, we have to bear in mind 1) that these solutions differ in osmotic value, and 2) that the various salts may have a particular effect on the structure of the protoplasm.

With regard to the difference in osmotic value, we may point out that the concentration of each of the two salts used in the experiments, was always 0.05 n, but that the osmotic value nevertheless differed to some extent. Unfortunately we had no sufficient data at our disposal to calculate these differences, and so their possible influence cannot be compared with the differences appearing in the table.

In Chapter II, § 1, when dealing with the spherical shape of the gymnoplasts, we have already pointed out that in order to maintain the structure of the protoplasm in a suitable condition KCl and $CaCl_2$ should be present in a definite proportion. Relatively little is known with regard to other salt mixtures, especially with regard to those containing the less common salts like CsCl, RbCl, etc. We should therefore consider the results of these first experiments, with much reservation. It might afterwards appear that in order to compare the effect of the various salt mixtures, it will be necessary to find out first in what proportion their influence on the protoplasm is as favourable as possible. This proportion will probably vary for the different proportions of the salts. Corrections will also have to be applied in connection with the differences in the osmotic value of the mixtures.

From the literature one does not get the impression that these points have often been taken into consideration. When the investigators wished to compare the influence of various salts on the permeability of the protoplasm, they confined themselves to plasmolysing the cells in solutions containing but one single salt, and on account of what has been said above, one can hardly expect that this will shed much light on the problem.

The sequence in which the salts can be arranged on account of their influence on the h.v.c. appears not to agree with that in which the elements are arranged in the periodic table. In many phenomena of colloid chemistry, however, the influence exercised by the various salts of the alkali metals and of the alkaline earth metals corresponds fully to what one would expect of them because of the position these metals occupy in the periodic table; in colloid chemistry this sequence is known as that of Hofmeister. TEUNISSEN (1936) and TEUNISSEN and BUNGENBERG DE JONG (1938) *et al* have determined at what concentration the various salts reverse the electric charge of a number of colloids, and found that for colloids with carboxyl or sulphate ions the sequence of the salts agrees with Hofmeister's series. However, for the phosphate colloids, the lecithins, to which they ascribe an important part in the structure of the protoplasm, deviations from this sequence were noted. This sequence, moreover, is not the same in all groups of phosphate colloids. According to these authors these deviations from Hofmeister's sequence would be a valuable argument in favour of the view that the plasma-membrane contains phosphatides, as for the latter too deviations of this kind have been reported. If the metals in the salts mentioned in Table XI are arranged according to the degree in which they lower the permeability of the protoplasm, we obtain the following sequences: in set *a* Rb $<$ Li $<$ Cs $<$ Na $<$ K and in set *b* Be $<$ Ba $<$ Sr $<$ Ca. It is not possible to determine the position of Mg, and with regard to the position of Li and of Be we will have to admit that it is rather uncertain. At any rate, the two sequences show similar deviations from the lyotropic sequence as the phosphatids did in the experiments of Bungenberg de Jong *et al.*, and this may therefore be adduced as an argument in favour of the views of these authors with regard to the structure of the plasma-membrane. In view of the incompleteness of our experiments mentioned above, it should be borne in mind that this argument cannot yet be regarded as sufficiently supported to be really conclusive.

CHAPTER IV

General discussion

§ 1. THE GYMNOPLAST AS A PHYSICO-CHEMICAL SYSTEM

For studying permeability the use of gymnoplasts, i.e. of protoplasts that have been freed from the surrounding cell wall, has doubtless some advantages above that of intact cells or tissue parts. In using gymnoplasts we need no longer consider the complications due to the filtration resistance of the cell wall, and to adsorption of part of the diffusing molecules in the latter, or those due to the presence of a "free space", which in recent times has been the object of many discussions (cf. G. E. BRIGGS and R. ROBERTSON, 1957). It is true that this free space might also contain a part of the cytoplasm itself, but this is a mere supposition, and as it is at the present moment impossible to test it experimentally, it hardly needs to be taken into consideration.

Even if we leave the possible existence of a free space in the gymnoplast out of consideration, the latter will have to be regarded as a complicated system. As to the structure of this system there is, however, as yet no uniformity of opinion, although the majority of the investigators assume that it consists, apart from the vacuole, of three layers: the ectoplasm, the central part of the cytoplasm and the tonoplast.

The number of investigators who doubt or even deny that the ectoplasm in the intact cell can be regarded as a layer whose physicochemical properties are different from the rest of the cytoplasm, continually increases (cf. ARISZ, 1945, and this author's review of the symplasm theory, 1956). According to these physiologists the ectoplasm would be formed during plasmolysis as an entirely new boundary layer of the protoplast, and would therefore be artificial. This would mean that the sharply defined ectoplasm observed in our gymnoplasts does not occur in intact cells, and that our gymnoplasts exhibit it because plasmolysis is an integral part of the method by which they are obtained. It should further be noted that no one so far has succeeded in separating the three layers without destroying the gymnoplast.

The presence of a substancial tonoplast was, in our experiments too, repeatedly observed when the gymnoplasts desintegrated, but their stability proved to be so low that it was impossible to use them for experiments. This rapid decay may perhaps be ascribed to the circumstance that the central mass of the cytoplasm no longer exercises its stabilizing influence on the orientation of the molecules in the tonoplast. In the experiments of LEVITT *et al.* (1936) and of KONINGSBERGER *et al.* (1947, b) the tonoplasts maintained themselves for a somewhat longer period. This may have been due to the circumstance that these investigators used a plasmolyte with a much higher salt concentration. Howsoever this may be, the conclusion that there exists, under natural circumstances, a relation between the molecular structure of the tonoplast and that of the adjoining layer of the cytoplasm, seems unavoidable.

This applies doubtless also to the ectoplasm. The classic argument against the view that the ectoplasm would be an artificial product caused by plasmolysis, is the presence of a clearly visible hyaline outer layer in naked protoplasts, e.g. in amoebae. The results of the experiments of CHAMBER and REZNIKOFF (1926) in which amoebae were injected with solutions of $CaCl_2$, seem to support this argument. In these experiments the protoplasm "solidified" in the vicinity of the place where the injection had been effected, and it tried to form a new hyaline membrane between the intact and this solidified part. However, according to more modern views the formation of the new membrane can be explained very well by assuming that the protoplasm because of dehydration (c.q. also of changes in electric potential) undergoes a "demixing" which, just as in plasmolysis, would lead to the formation of a membrane.

A second, somewhat similar argument for the independent existence of the ectoplasm, may be found in observations made by PLOWE (1931), who drew plasma threads from the ectoplasm of protoplasts that had been isolated from onion cells. She saw herein a proof of the elasticity of the substance of which the ectoplasm consists. Similar observations were repeatedly made in our experiments too. It was further noted that when the ectoplasm was damaged, the whole gymnoplast succumbed. However, these experiments too were made with protoplasts that had been isolated by means of plasmolysis. It should be noted, moreover, that Plowe as well as we ourselves observed sometimes how parts of the granular cytoplasm were carried along with the threads in the form of swellings. Interesting as these observations are in themselves, they certainly do not prove that the ectoplasm was already present as a substancial membrane in the intact cells.

We should however bear in mind that in the large majority of the investigations dealing with the permeability for water, use has been made of the plasmolytic method. Only in a single instance (KAMIYA and TAZAWA, 1956) the permeability for water was measured by means of a different method. It is noteworthy that the results obtained with their method i.e. by applying transcellular osmosis, did not differ qualitatively from those obtained by the aid of the plasmolytic one.

HÖFLER (1931) gave a clear definition of the term permeability, but subsequent investigators (BOGEN, 1956; CURTIS and CLARK, 1950; BUNGENBERG DE JONG, 1947) have used it in a somewhat different way. For this reason we wish to state emphatically that when in the present paper the term is used, the permeability of the whole system consisting of the ectoplasm, the central layers of the cytoplasm and the tonoplast, in one direction or the other, and for the dissolvent as well as for the solutes, is meant. As we worked with gymnoplasts only, the permeability of the cell wall (according to Höfler's definition) was left out of consideration.

In this paper we have confined our attention to the permeability for water. For a quantitative study of the latter it is necessary that the concentration of the medium as well as that in the vacuole remain constant during the course of the experiment, i.e. that dissolved substances do not pass the protoplasm. As in each of the solutions the volume of the gymnoplasts remained constant for a long time, we may conclude that this condition was fulfilled. The differences in the degree of permeability caused by differences in the composition of the medium may therefore be ascribed to changes in the diffusion resistance of the system ectoplasm, cytoplasm proper, tonoplast, i.e. to changes in the structure of this system.

Above we have already mentioned that the three component parts of this system are so intimately united that it is impossible to separate them without destroying the gymnoplasts. By simple inspection it is therefore impossible to decide which of the three components is to be regarded as responsible for the change in the degree of permeability. Physiological means to this end are inadequate too. When the temperature is changed, this will affect the whole system, although it is not improbable that the three components will all of them react in their own way. This applies also to the action of the various plasmolytes and their constituent parts.

When we attempt to use the results of our experiments in order to elucidate the part played by the three components of the protoplasm in the changes of the degree of permeability, it is clear that we will have to leave the domain of ascertained facts and enter that of the hypotheses. Here we will have to base our conclusions on the various theories that have been proposed with regard to the submicroscopic structure of the three components of the protoplasm and their physicochemical properties. In the following pages we will therefore pass in review those theories that for our purpose seem to be of most importance.

As far as the boundary layers of the protoplasm are concerned, the lipoid theory of OVERTON (1895, 1899), in its modern framing, is of particular importance. HANSTEEN CRANNER (1922) was the first to note that when roots of different plant species were immersed in salt solutions of various composition, lipids were exuded into the medium; no proteins, however, were found in the latter. The lipids were supposed to originate from the plasmalemma. Later on GRAFE, HORVATH and MAGISTRIS (1925, 1926) reported the presence of lecithin-like compounds among these lipids.

Against the lipoid theory, which postulates affinity between the permeating substances and the compounds of which the membrane consist, the filter theory assumes submicroscopic pores in the membrane, through which permeating substances are allowed to pass.

As a matter of fact, the structure of the protoplasmic membrane has to answer both demands. It must account for the permeation of polar hydrophobic substances, which permeate more readily the more hydrophobic the compound. At the same time it should be such that small hydrophilic ions cannot pass or pass only with great difficulty, whereas the much larger hydrophilic molecule of glycerol permeates rather easily.

A structure that complies with these two, at first view incompatible, demands, has been suggested by BUNGENBERG DE JONG, BOOIJ and several co-workers (for surveys cf. 1947 a, 1949 and 1956).

As early as 1926 GORTER and GRENDEL, when extracting erythrocytes, obtained lipids that proved to spread over a water/air interface. They calculated from the dimension of the surface occupied by this monomolecular layer and that of the surface of the erythrocytes that the latter might be coated by a double layer of these lipid molecules. In 1932 BUNGENBERG DE JONG advocated that lipids like lecithin and cholesterol would preferably accumulate in the interface protoplasm/water (for recent arguments cf. BOOIJ and BUNGENBERG DE JONG, 1956 and BOOIJ, 1956).

In connection with his complex theory Bungenberg de Jong in collaboration with his co-workers developed the view that the boundary layer of the protoplasm would consist of at least one lecithin-coacervate film two molecules thick. The orientation of these lecithin molecules would be such that the apolar lipophilic radicals would be situated at the water- and protoplasm-sides, whereas the hydrophilic ionogenic groups would lie inside the film. According to Bungenberg de Jong such a system would owe its stability to three factors, viz. (1) the London–van der Waals' attraction forces between the apolar radicals, (2) electric attraction forces (Coulomb forces) between the ionised groups, and (3) hydratative repulsion between the latter. The last-named factor has to be regarded as a stabilizing agent, as in its absence the film would flocculate. When small quantities of other lipids, particularly of cholesterol, are added, their molecules will insert themselves between the apolar radicals, and in this way reinforce the London–van der Waals' attraction; such substances would act as "sensitizers". The Coulomb forces are, of course, to a high degree dependent upon the presence of ions, as the latter strongly influence the charge of the ionized groups.

For our purpose it is of particular interest that TEUNISSEN (1936) and TEUNISSEN and BUNGENBERG DE JONG (1938) determined the concentrations of different cations that are required to discharge various biocolloids. When the required concentrations of the various cations are plotted according to their equivalency, a so-called ionic spectrum is obtained. For biocolloids with sulphate or carboxyl groups as ionized radicals the sequence of the cations in this spectrum proved to agree with that in Hofmeister's lyotropic sequence. For phosphate colloids, the group to which the lecithin coacervates belong, deviations were found, which means that here transition sequences occur. Similar deviations were found in the experiments described in this paper (Ch. III, § 7 and Ch. IV, § 4.).

BUNGENBERG DE JONG (1949) ascribed this particular character of the action of the various cations on the biocolloids to the valency, radius, and polarizing power of the inorganic ions and to the polarizability of the ionogenic groups of the particular colloid and of the water. When we confine ourselves for the moment to the cations, this means that the polarizing power increases with the size of the atoms from which they are derived, in the following sequence therefore: $Li < Na < K < Rb < Cs$. The smaller the atom, the stronger the hydratation of its ion, and the weaker the electric field force exercised by the latter. For small atoms this field force is too small to exercise an appreciable polarizing activity.

Another important argument in favour of Bungenberg de Jong's conception is that it readily accounts for the phenomenon of ionic antagonism. BUNGENBERG DE JONG, BOOIJ and WAKKIE (1936) found in phosphate colloids (lecithin), but not in biocolloids belonging to other groups, an antagonistic effect between KCl and $CaCl_2$, which proved to be the more pronounced the purer the lecithin preparation.

Bungenberg de Jong soon recognized that his first model was too static and too rigid to account for the diversity of the reactions found in the living protoplasm. He therefore suggested that the protoplasmic boundary layer would contain, besides lecithin, free phosphatide-acid molecules, i.e. that it would be a tri-complex system. It is noteworthy that MEYER (1957) recently found free phosphatide-acid in the cells of the onion bulb; this substance might quite well arise from a partial hydrolysis of lecithin. The ratio between lecithin and free acid would largely depend upon seasonal factors.

BOOIJ and BUNGENBERG DE JONG (1956) assume that in the central part of the cytoplasm lecithin too is present, and serves as a stock for supplying the peripheral part. Such a ready supply would account for the fact that the boundary membrane can change its form and its dimensions in a very short time, as we see e.g. when an amoeba puts out pseudopodia, or when a damaged cell regenerates its membrane.

That the structure of the boundary layer would be so simple as it was supposed to be by Bungenberg de Jong *et al.*, was soon questioned. HARVEY and DANIELLI (1936) argued that the surface tension between protoplast and water might be expected to be similar to that found in the interface between oil and water. In their measurements, however, the surface tension between protoplast and water proved to be much lower. To explain this difference they supposed that the coacervate film of lecithin would be covered on both sides by a protein layer. This view found support in measurements of the degree of elasticity; in the protoplasmic membranes the latter was found to be much higher than in lecithin coacervates, but lower than in proteins; the values found for mixtures of proteins and lecithin proved to be intermediary.

From his experiments with erythrocytes, WINKLER (1938) derived several arguments for the view that in the protoplasmic membranes a lecithin coacervate film is linked to proteins.

According to the at present accepted view, lecithin-like phosphatides, and perhaps some other lipids, form, together with proteins, the principal structural components of the protoplasmic boundary layer, whereas ions, e.g. K^+ and Ca^{++}, are responsible for the electric charge of the ionogenic groups and in this way regulate the hydratation of the membranes and the magnitude of the attraction forces in the latter. There is, however, a certain degree of competition between these ions, especially between K^+ and Ca^{++}, the so-called ionic antagonism, and it is on account of this antagonism that K^+ as well as Ca^{++} prove to be indispensable The required Ca^{++} concentration may, however, be very low. ALBACH (1931) found that the tap water he used in his experiments, contained enough Ca^{++} to maintain the protoplasm in a normal condition.

At present there is no proof that there are anything but quantitative differences between the composition of the ectoplasm and that of the tonoplast. The presence of quantitative differences, on the other hand, cannot be doubted. After alkaline saponification of the lipids in the cells of onion bulbs GICKLHORN (1932) found that the myeline figures indicated that the lipid content of the tonoplast is higher than that of the ectoplasm. The differences in the rate of intrability and permeability, and phenomena like cap plasmolysis and abnormal plasmolysis, nevertheless suggest qualitative differences in the structure of tonoplast and ectoplasm, but these features have not yet been sufficiently elucidated.

In comparison to the great interest the investigators of the protoplasm have shown in the composition and structure of the boundary layers, but little has been said on the remaining part of the cytoplasm. Chemical analysis shows the presence of organic compounds, mainly proteins and lipids (lecithin), and some inorganic salts. It must be in a colloidal state, since investigations of its elasticity and viscosity proved that it does not behave as a Newtonian liquid. The viscosity of such a liquid is independent of external pressure, but PFEIFFER (1936) showed, by pressing gymnoplasts obtained from onion cells through narrow capillaries and estimating the degree of viscosity by observing the Brownian movement inside the cytoplasm, that the viscosity of the latter is to a considerable degree dependent upon the pressure exerted on the gymnoplast; in droplets of glycerol that served as a control, it remained the same under these circumstances. The cytoplasm therefore behaves like an "elastic solution", but this does not imply that it has a definite structure (FREY WYSSLING, 1953).

The fact that it is possible to draw threads from the cytoplasm, also forbids us to regard the latter as a Newtonian liquid, for the formation of such threads requires that at least the surface is a gel. When such a thread is released, it is withdrawn into the protoplast. Particles of cytoplasm may move into the threads, which suggests that at least parts of the cytoplasm are in a liquid state. The inner part therefore would have to be regarded as a sol. The phenomenon known as "protoplasmic streaming" points in the same direction. MARSLAND (quoted on the authority of FREY-WYSSLING, 1955) in studying the Brownian movement in *Amoeba* came to the conclusion that the streaming is confined to the inner part of the protoplast, and that it does not occur in the ectoplasm because the latter is a gel.

CRICK and HUGHES (1950) introduced minute particles of iron into the fibroblasts of a chick, and then shifted them a little from their position by means of a magnet. When the latter was removed, the particles returned to their former position, although they did not at once come to rest but kept on vibrating for some time. These experiments remind one of those taken by BUNGENBERG DE JONG, VAN DEN BERG and VREUGDENHIL (1949) in order to demonstrate the elasticity of oleate systems. The oleate coacervate was rotated in a glass vessel after some airbubbles had been introduced into it. When the rotation was stopped, the airbubbles kept on vibrating for some time, and this time proved to vary in different oleate systems, which apparently means that their degree of elasticity is different.

As SEIFRIZ (1952) has pointed out, elasticity should not be confused with viscosity, and especially in biology these terms should be used more cautiously then they now often are. The cause of the trouble lies in the circumstance that the state of aggregation met with in biological objects, is often difficult to determine. In cases of uncertainty it is best to speak of a "structured" substance.

On the old question "is the cytoplasm a sol or a gel" FREY–WYSSLING (1938, 1953, 1955) passed a Solomonian judgement. He convincingly argues that both states of aggregation must be coexistent, and that plasmasol can and will continuously be converted into plasmagel, and vice-versa. A structureless sol and a rigid gel are states that are incompatible with the living protoplasm, and the presence of one of them alone is a sure sign of death. That the macromolecules of the protoplasm can at any moment and at any place dissociate to form a sol, or aggregate to turn into a gel, must be considered characteristic for the dynamic living state.

The viscosity of an albumen sol is much lower than that of the living protoplasm. According to FREY–WYSSLING (1953, 1955) this proves that the cytoplasm can not consist of free spherical macromolecules only, but that fibrous elements must be present. For this idea, which was published for the first time in 1938 in the German edition of his work on the submicroscopical structure of the protoplasm, support was found in electron microscopic photographs of the protoplasm (FREY–WYSSLING and MÜHLETHALER, 1944, BRETSCHNEIDER, 1951, 1952, *et al.*).

According to Frey-Wyssling the dynamic character of the living protoplasm would largely be due to the fact that the fibrous polypeptide chain molecules, by ever changing the "junctions" between their side chains, can form aggregates with each other and with other colloid molecules. By the formation, respectively the severing, of such junctions, reversible transitions from sol to gel are possible. These changes would largely be governed by external conditions, and it would be in this way that the latter exercise their influence on the consistency of the protoplasm. In 1938 FREY–WYSSLING already postulated four types of junction, viz.

(1) *homopolar cohesive bonds*, i.e. mutual attraction of lipidic groups (of the character of London–van der Waals' forces), and sensitive to *temperature* changes;

(2) *heteropolar cohesive bonds*, i.e. attraction between groups of pronounced dipole character; to which also belong the so-called *hydrogen bridges*, sensitive to *hydratation* changes, i.e. the ions, present within the radius of the ionogenic group;

(3) *heteropolar valency bonds*, i.e. formation of salts and esters, and sensitive to changes of *pH*;

(4) *homopolar valency bonds* or bridge formation, dependent on the *redox potential* of the system.

This theory, which accounts for several properties of the living protoplasm and for the way in which they depend upon external factors, has met with criticism. Booij and Bungenberg de Jong (1956) doubt whether the life-time of the various types of attraction would be long enough (bonds 1–3) or too long (bond 4) to regulate the transition from sol to gel and vice-versa.

As a matter of fact, such transitions occur in the living state, and have in several instances been ascribed to the mediation of the ATP, (adenosine-triphosphate), system. Goldacre and Lorch (1950) regarded the movements of *Amoeba* as caused by changes in the contractability of the protoplasm, and they suppose that the gel-sol equilibrium in the latter continuously changes under the influence of the ATP system. Ts'o, J. Bonner, Eggman and Vinograd (1956) discovered a RNA (ribo-nucleic-acid) protein system (myxomyosin) that proved to be sensitive to ATP in the plasmodium of *Physarum polycephalum*. They also found that in this plasmodium two different kinds of viscosity may be present, viz. (1) the normal viscosity that is characteristic for a solution of strongly hydrated colloids, and (2) a "structural viscosity" due to the formation of aggregates between the dissolved molecules. The second kind of viscosity is apparently due to the presence of the ATP system.

The view that such changes in structure may play an important part in the life of the protoplast, finds a strong support in the results of investigations carried out by Astbury, Perry, Reed and Spark (1947) and by Astbury (1947–1949). By means of electron microphotographs they showed that at pH 7 and in the presence of 0.1 mol KCl, G-actin (globular actin) passes into F-actin (fibrillar actin). Moreover, when F-actin and myosin are mixed in the ratio 8 to 1, the electron microscopic image shows a clear gel structure; the latter, however, disappears after addition of 0.0013 mol ATP. These changes in structure are accompanied by changes in the degree of viscosity that are similar to those recorded in the work of Ts'o *et al.* for the plasmodia of *Physarum polycephalum* in the presence of ATP. Astbury *et al.* suppose that sulphydryl radicals are involved in the interaction between myosin and actin, and that the latter are closely related to the action of ATP. It therefore seems clear that the physico-chemical state of the protoplasm depends in a large measure on particular biochemical processes.

Booij and Bungenberg de Jong (1956) further objected against Frey-Wyssling's views on the structure of the cytoplasm, that they do not pay sufficient attention to the presence of association colloids like lecithin. Their presence, however, should not be neglected, as they may influence the viscosity and the elasticity of the protoplasm. They tried to prove this by a study of the behaviour of onion cells in solutions of KCl and of $CaCl_2$. They began by pretreating these cells in solutions of these salts, and then plasmolysed them in a sucrose solution. After the pretreatment with KCl the plasmolysis proved to be of the convex type, and after that with $CaCl_2$ of the concave type. However, this does not really prove that these salts exercise an influence on the association colloids inside the cytoplasm, as there is no certainty that the K- and Ca-ions actually penetrated into the latter.

Booij and Bungenberg de Jong further drew attention to the fact that, according to HÖFLER (1939/1940), cap-plasmolysis can be obtained by leaving the cells for a considerable time in a hypertonic solution of KNO_3, but that it disappears in a solution of $CaCl_2$ of the same concentration. This would prove that the lecithin colloids play a more important part in the cytoplasm than the protein colloids. HOFMEISTER (1954), however, pointed out that K-ions might weaken the junctions between the polypeptide molecules in the various layers of the cytoplasm, whereas Ca-ions would have the opposite effect. This is in agreement with the observation recorded in the present paper that the gymnoplasts in the dextrose solutions that contained only KCl showed a tendency to fuse. It is possible, therefore, that the K-ions in penetrating into the cytoplasm, diminish the aggregation of the protein colloids, and by increasing their hydratation cause a swelling which manifests itself in the cap-plasmolysis.

The preceding considerations show that Frey-Wyssling's junction theory as well as the coacervation theory developed by Bungenberg de Jong *et al.* help us to understand several aspects of the behaviour shown by the living protoplasm. There are, however, certain incompatibilities between the two theories that will have to be eliminated, and if we should succeed in doing this, it is to be expected that we will obtain an even better idea of the nature of the protoplasm.

For the interpretation of our results the thickness of the cytoplasm layer is a factor of importance. Very little, however, is known of the thickness of this layer in plant cells. BARER (1953) succeeded in determining, by the aid of the phase-contrast microscope, the thickness of the cytoplasm layer in cells obtained from the epithelium of the human mouth. This method might perhaps be applied also for determining the changes in thickness this layer undergoes in plant cells, and if we succeeded in doing this, we would be in a position to study the relation between these changes and the concomitant changes in the permeability of the protoplasm for water. However, it does not seem likely that such changes in thickness will have exercised a marked influence on the results of the experiments described in the present paper.

The concentration of the salts in our plasmolyte, whose osmotic value rested for the main part on the presence of 0.66 mol dextrose, was rather low, and there were, as a rule, no indications that the salts penetrated into the inner part of the cytoplasm, and that they changed the latter's colloidal state. Only in those cases where the gymnoplasts succumbed, matters may have been different, for here too strong a hydratation may, with fatal results, have shifted the sol-gel equilibrium to the right.

However, even if it should appear that the ions in the plasmolyte, under normal circumstances too, would be able to effect such a shift in the gel-sol equilibrium of the plasma colloids, it would be impossible to decide whether this shift, which would be responsible for an increase in the permeability for water, took place in the plasma-membranes or in the inner layers of the cytoplasm.

§ 2. THE GYMNOPLAST AS AN OSMOTIC SYSTEM

In Ch. III, § 4. we have described our experiments on the influence exercised by plasmolysis and deplasmolysis on the volume changes of the gymnoplasts. The results of these experiments allow us to discuss the following three points, viz.

A. the relation between the osmotic value of the medium and the volume of the gymnoplasts at a constant temperature;

B. idem at different temperatures; and

C. idem when the ratio between the cation concentrations in the medium is changed, while temperature and osmotic value are kept constant.

A. Relation between osmotic value and gymnoplast volume

Fig. 12 shows the results of our experiments. As stated in the description former, the curve shown in this figure represents the relation between the osmotic value of the medium and the volume of the gymnoplasts as it would be if the latter obeyed van 't Hoff's law. At first sight the values that were actually observed, do not seem to differ from the calculated ones, but a closer inspection reveals that the volume of the expanded gymnoplasts, i.e. that reached at the end of the partial deplasmolysis, is, with a single exception, always smaller than the expected one, whereas that of the contracted gymnoplasts, i.e. the one reached by plasmolysis, is in 31 % of them larger, and in 69 % smaller.

So far the explanation of the osmotic behaviour of protoplasts has always met difficulties. HÖFLER (1920) came, in his study of the relation between osmotic value, suction force and turgor in the plant cell, to the conclusion that van 't Hoff's law is valid only if the thickness of the cytoplasma layer in comparison with that of the cell can be regarded as thin. To adapt van 't Hoff's law to the plant cell, CUTCHEON *et al.* (1931) proposed to introduce in the equation, after the example of PORTER (1917), a factor b, which has to be subtracted from V; in this way van 't Hoff's law becomes $\pi (V - b) = C$. The factor b represents the sum of the volume of the osmotically active substances in the protoplasm, i.e. the dissolved ones, and that of the osmotically inactive material, i.e. the cytoplasm proper. As the volume of the dissolved substances is very small in comparison with that of the inactive ones, it may be neglected. CUTCHEON *et al.* (1931) and RESÜHR (1935) assumed that the osmotically inactive part of the cytoplasm remains constant. This was found by them in the eggs of *Arbacia*, where, however, by far the greater part of the cell consists of cytoplasm. Entirely different results might be obtained with cells in which the greater part of the volume is occupied by the vacuole, but where the layer of cytoplasm is not yet so thin that it may be neglected; in such cells a change in the sol-gel equilibrium of the cytoplasm might very well influence the ratio between the total volume of the protoplast and that of the cytoplasm. DE HAAN (1933) and LEVITT *et al.* (1936) actually found that the protoplasm of onion cells and gymnoplasts may show a considerable swelling under the influence of salts. They consequently found a continuous variation of the factor *b*. BOGEN and PRELL (1952) came to the same conclusion in their study of the osmotic behaviour of epidermal cells from the stems of *Oenothera*, where the actually observed volumes of the protoplasts were larger than the calculated ones. HÖFLER (1939/40) found a marked increase in the thickness of the cytoplasm layer in onion cells that showed cap-plasmolysis. Since this phenomenon could not be ascribed to osmosis, he tried to explain it by an extra water uptake due to a high swelling force of the plasma colloids. A drawback of his experiments is that he used rather concentrated KNO_3 solutions, which will have exercised a strong influence on the structure of the protoplasm.

In studying the osmotic behaviour of erythrocytes, PONDER (1944) too found deviations from van 't Hoff's law. In order to explain the latter, he recognized three possibilities, viz. (1) there is an exosmosis, endosmosis, katatonosis or anatonosis; (2) the amount of water that is bound in the colloids varies under the influence of salts; and (3) there are elastic forces, resting on the structure of the protoplasm, which oppose the entrance of water or favour its exudation.

When we try to find out whether the deviations found in our own experiments on the osmotic behaviour of onion gymnoplasts can be explained in one of the three ways suggested by Ponder, it appears that the first way, at any rate, is to be considered improbable, as the final volume remained constant for a long time. This was found especially in the experiments with solutions containing K- and Ca-salts.

The second way suggested by Ponder will have to be formulated somewhat differently, when we wish to apply it to our own experiments, because in the latter the gymnoplast volume did not change under the influence of the salt concentration, which was kept constant, but under that of the dextrose concentration. The dextrose dehydrates the protoplasm, and this may lead to a change in its structure, e.g. by shifting the sol-gel equilibrium. According to FREY–WYSSLING (1953–1955) an isothermic transformation of a sol into a gel may influence the volume of the substance in three ways; the volume may decrease, it may remain the same, or it may increase.

A decrease in volume has, as far as we know, never been observed in the protoplasm. Frey-Wyssling, moreover, adduced arguments which make it improbable that it would occur here. When a gel is formed, the hydratation at several of the "junctions" will decrease, and this means that water is set free. It is doubtless more probable that this water will increase the gel volume than that it will reduce it.

The volume would remain the same when the protoplasm behaved like a thixotropic colloid. In that case the transformation of sol into gel is obtained by stirring or shaking; it takes place within a wide range of temperatures, and is not influenced by the latter. This cannot be said of the results obtained in our experiments, as the latter appeared to be strongly dependent upon temperature.

It seems therefore probable that for protoplasm the transformation of a sol into a gel will be accompanied by an increase in volume. In our experiments the volume of the gymnoplasts exceeded the theoretical volume in the neighbourhood of the starting point only. One might be inclined to assume that exactly in this region the sol-gel equilibrium would be shifted further to the right than anywhere else, and that here the major part of the protoplasm would be in a gel state. It is, however, hard to understand why at higher concentrations the observed volume is always smaller than the calculated one. It seems sophisticated to assume that this should be due to a shift of the sol-gel equilibrium to the left.

It seems therefore far more probable that the deviations of our volume curve from the theoretical one mainly are due to forces suggested by Ponder sub (3): i.e. elastic forces whose presence is due to the particular structure, viz. the "structural viscosity" of the protoplasm.

Before leaving this subject we wish to point out that the interpretation of the results obtained after a repeated transfer from a hypotonic to a hypertonic solution requires great caution. In section 4 of chapter III we described how the gymnoplasts often undergo considerable changes in shape before they reach the final spherical shape. This made it impossible to measure the intermediate ones accurately, and for this reason it was impossible to express the exact course of the change in figures.

B. Gymnoplast volume and temperature

Fig. 13 shows the results of our experiments on the influence of temperature on the final value of the volume reached by the gymnoplasts after the medium had been diluted, i.e. after deplasmolysis.

At all temperatures higher than 2° C the observed values prove to differ quite conspicuously from the calculated ones. The value found for 2° C is the only one that agrees with the calculated value. The difference between the observed and the calculated value reaches its maximum at 20° C. Above that temperature the difference decreases.

It is noteworthy that the ratio between the concentration of the two kinds of ions in the medium was the same in all three sets of experiments. It is true that on account of the different temperatures there were nevertheless small differences in the osmotic value of the medium, but these differences were certainly not large enough to explain the differences between the observed and the calculated value of the final volume. Moreover, if the difference between the observed and the calculated values really depended upon these differences in the osmotic value of the medium, they should increase regularly with the temperature, and this is not so.

Hartmann (1919) devoted a special study to the influence of temperature on the magnitude of the volume of the cell and of its nucleus; to this end he used a.o. epidermal cells of *Allium*. In this study the difference between the observed and the calculated values of the volume was found to depend in the same way on temperature as the corresponding difference in our own experiments. He supposed that this difference would be caused by the presence of temperature-dependent processes in the protoplasm, but he was unable to define the latter more precisely. He suggested, however, some possibilities, e.g. changes in osmotic values, or in the degree of swelling of colloids, or the shifting of chemical equilibria.

As we have shown in Ch. III, § 4, the permeability for water increases strongly with a rise of temperature, at least up to 36° C (Fig. 10), the highest temperature that was used in our experiments. The curve that expresses this relation, is entirely different in shape from that of Fig. 13, which shows how the difference between the observed and the calculated values of the volume depends upon temperature. This means that there is no reason to look for a close relation between the way in which temperature affects the changes in osmotic behaviour, i.e. in the permeability for water, and that in which it influences the changes in the final value of the volume. A shifting of various chemical equilibria, in the first place of the sol-gel equilibrium, in the protoplasm, is probably responsible for the differences between the observed and the calculated values of the final volume.

As we have already mentioned in section 1, facts have recently come to light that seem to indicate an important influence of the ATP system on the physico-chemical state of the protoplasm. The protoplasm might mainly consist of a gel at the lower temperatures, but a rise of temperature would, by enhancing the activity of the ATP system, shift the equilibrium in the direction of the sol state. As we have pointed out above, such a shift of the gel-sol equilibrium to the right would be accompanied by a decrease in volume. At 20° C this shift to the right would have reached its maximum value.

Levitt (1941) and Scarth (1944) in their studies on the problem of cold resistance explained this resistance in a similar way by assuming that the protoplasm at decreasing temperature passes more and more into a gel state, and that this is accompanied by an enlargement of the protoplast.

More difficult to explain is the increase in gelation at temperatures above 20° C, as in non-living systems no examples of gelation at higher temperatures are known. The results of experiments taken by Astbury *et al.* (1947) are, however, of great importance for our purpose. In these experiments it appeared that F-actin may maintain itself at 60° C in the β-configuration, which is a linear-fibrillar form of the protein combination chain keratin-myosin-epidermis-fibrinogen, (k-m-e-f-protein), used in their experiments. The linear shape of the protein molecules will obviously lead to gelation. It may, however, be objected that these are experiments with non-living models. A phenomenon, however, that seems to point in the same direction, is the stopping of the protoplasmic streaming at higher temperatures, which might be due to a shift of the sol-gel equilibrium to the right. GOLDACRE and LORCH (1950) and GOLDACRE (1952) rightly remarked that the protoplasm can only be in motion as long as it is a sol.

In the experiments of which the results are shown in Fig. 13, the media, however, were not fully comparable, as they were obtained in two ways, viz. by diluting the original solution (1) with water (Fig. 13 *a* and Fig. 13 *b*) and (2) with a salt solution in which the salts were present in the same concentration as in the undiluted solution; in media obtained in the latter way the concentration of the dextrose alone was lowered (Fig. 13 *c*). Qualitatively this made no difference in the results.

If the ATP system really influences the sol-gel equilibrium in the protoplasm, this influence must be larger than that exercised by the difference in the composition of the medium caused by the way in which the latter was diluted. The lower ion concentration in the set of experiments of which the results are shown in Fig. 13 *b*, has but a slight influence on the position of the sol-gel equilibrium; this is apparent when we compare Fig. 13 *b* with Fig. 13 *c*.

Much larger is the difference between Fig. 13 *a* and Fig. 13 *b*. In the experiments of which the results are shown in Fig. 13 *a* the plasmolyte contained 0.04 n KCl and 0.045 n $CaCl_2$, in the experiments of Fig. 13 *b* 0.09 n KCl and 0.04 n $CaCl_2$. The differences between the results of the two sets of experiments may be due to the following causes, viz. (1) the difference in the salt concentrations in the medium; (2) a seasonal difference; and (3) a different electro-endosmosis.

That the differences would be due to the first-named cause, does not seem likely, the differences in salt concentration being too small. One might, on the other hand, be inclined to ascribe them to the second cause, a seasonal difference, which in other experiments too proved to be considerable. The equilibrium sol-gel might easily occupy different positions in the various parts of the year. In onion cells the protoplasm may be more strongly gelated in January and February, which is the resting season of the bulbs, than towards the end of the summer when the cells still show all sorts of activities. At that time the sol-gel equilibrium would lie further to the left, and the difference between the observed value of the volume and the calculated one would be larger.

The difference in the concentration of the two salts that are present in the medium, suggest the possibility that electro-endosmotic forces arise and cause an extra water uptake (cause 3). This possibility will be investigated sub *C*.

C. Relation between volume and salt ratio when osmotic value and temperature of the medium remain constant

In order to investigate the possibility of an electro-endosmosis we must first study the influence exercised on the final value of the volume by plasmolytes containing a constant concentration of dextrose viz. 0.66 mol and varying concentrations of KCl and $CaCl_2$ of which the sum, however, always amounted to 0.1 n. The osmotic value of these solutions was therefore practically the same. The results of the experiments we took to determine the influence of these plasmolytes, are expressed in Fig. 14.

In view of the fact that there are no indications that salts would have penetrated into the protoplasm, and realizing that these experiments were taken at a temperature of 24° C, at which, as we have seen, the shifting of the sol-gel equilibrium to the left has about its highest value (cf. Fig. 13), it appears impossible to ascribe the results to changes in the sol-gel equilibrium in the protoplasm. We will therefore have to look for another explanation, and this might, in our opinion, be found in a change of the electro-endosmotic forces.

Bogen and Prell (1952) and Bogen (1953) have shown that electro-endosmotic forces may increase the effect of the osmotic forces in the strict sense, so that more water is absorbed than one would expect on account of the strength of the latter, and the actually observed increase of the cell volume accordingly is larger than the calculated one. For the explanation of these osmotic anomalies they tried to find support from Studener (1948). Other investigators too (Bennet–Clark and Bexon, 1943/46, Brauner and Hasman, 1943/47, Crafts, Currier and Stocking, 1949, and Frey–Wyssling, 1955) draw the attention to the possibility that the explanation of anomalies in osmotic behaviour may be found in the field of electro-endosmosis.

The dextrose concentrations which Studener used in her experiments with onion cells, were nearly the same as ours, but she applied lower salt concentrations. She found that the ζ-potential of the plasma-membrane depends upon the salt concentration in the medium. These potentials would be neutralized to some extent by raising the salt concentration of the medium to a value of 0.01–0.05 mol and this would lead to the exosmosis of a corresponding amount of water and a decrease in volume of the protoplast.

A similar effect on the electric potentials of interfaces is also known from the investigations of Bungenberg de Jong *et al.* (1936) on the influence of salts on the charge mosaics of complex coacervates. They found that univalent as well as bivalent cations affect the charge of this mosaic, but that in a mixture of them the effect is smaller than one would expect. A similar antagonism played a part in our own experiments with mixtures of KCl and $CaCl_2$, where it reached its maximum value when the concentration of each of the two salts was 0.05 n. At that point the membrane potential of the gymnoplast would have such a low value that no water is taken up by electro-endosmosis. Why at this point the observed value does not fully agree with the one calculated on the base of van 't Hoff's law, has been explained under *B*. Here the sol-gel equilibrium plays a part.

When the ratio between the salt concentrations is changed, the electro-endosmotic force at once begins to increase; this means that extra water is taken up and that the volume accordingly increases.

In this way it becomes possible to explain why in fig. 13 the difference between the observed value of the volume and the calculated one is smaller in a plasmolyte containing 0.09 n KCl and 0.04 n $CaCl_2$ than in one with 0.04 n KCl and 0.045 n $CaCl_2$. In the first case the electro-endosmotic force is much larger, and so the amount, of water that, in addition to the normal amount is taken up, and the extra-increase in volume of the gymnoplast is also larger.

§ 3. EFFECT OF TEMPERATURE ON PERMEATION RATE OF WATER

The results of the experiments on the effect of temperature on the speed with which water passes the protoplasm, are expressed in fig. 10.

This effect is doubtless of a complex kind, for all processes that play a part in the uptake of water and in its passage through the protoplasm, will be simultaneously affected by temperature in one way or another. It is therefore of importance to know what processes actually are involved, and in what way they are affected.

According to the complex theory of Bungenberg de Jong the permeability for hydrophilic molecules (e.g. sugars) is determined by the distribution of larger and smaller pores between the molecules of the plasma-membrane in molecular motion. A rise in temperature increases the motion of these molecules, and also causes an increase in the number of pores. The increase in number of the two kinds of pores will, however, exercise little influence on the permeation of the much smaller water molecules, and we cannot expect that the permeation rate will in this way be strongly influenced by temperature.

Our experiments prove that the temperature coefficient (Q_{10}) is relatively low (Table VI), but nevertheless much higher than that of a diffusion process. Further it is noteworthy that the decrease of the Q_{10} at increasing temperatures is stronger when the medium contains besides dextrose 0.04 n KCl and 0.045 n $CaCl_2$ instead of 0.09 n KCl and 0.04 n $CaCl_2$ (cf. Table VI). A similar difference in the decrease of the Q_{10} at higher temperatures has been reported by DELF (1916) for Dandelion cells. For onion cells, however, this author found a continuously increasing Q_{10}, although the rate of increase showed a diminution at the higher temperatures. It should be noted that her method differed from ours; for she determined the permeability for water by measuring the speed with which the volume of turgescent tissue decreased in a plasmolyte.

In the preceding section (§ 2, *B* and *C*) we have argued that the uptake of water is governed by three factors, the sol-gel equilibrium in the protoplasm, osmotic forces in the strict sense and electro-endosmotic ones. The activity of the osmotic forces proper is not strongly influenced by temperature and its Q_{10} therefore is low; it is that of a diffusion process. The effect of a rise in temperature on the sol-gel equilibrium in the protoplasm is, as we have seen, of more importance. A shift in the equilibrium to the right will increase the resistance the flow of water has to overcome in its passage through the protoplasm, and this will manifest itself in a decrease of the Q_{10}. However, this cannot be the only factor that has to be taken into account, for if we compare Table VI *a* with Table VI *b* it appears that the Q_{10} decreases more strongly in a medium containing 0.04 n KCl and 0.045 n $CaCl_2$ than in one containing 0.09 n KCl and 0.04 n $CaCl_2$. In section 2 *C* we have argued that the electro-endosmotic forces in the gymnoplasts in the second medium must be larger than those in the gymnoplasts in the first one. The Q_{10} of electro-endosmotic processes is known to increase with the temperature (FREUNDLICH, 1923), which does not apply to the Q_{10} found in our experiments. However, the fact that the decrease is smaller in the experiments in which the electro-endosmotic forces are on good grounds assumed to be higher, indicates that these forces really play a part.

The Q_{10} found in our experiments is the resultant of the interaction of the Q_{10}-s of the various processes that are involved. As in the gymnoplasts lying in the first medium electro-endosmosis plays a subordinate part only, the decrease of the Q_{10} will here be due to the predominating influence of the gelation of the protoplasm. In the second medium the influence of the latter factor is to some extent counteracted by the increase of the electro-endosmosis.

In our own experiments the influence of the season may also have played a part, as the second set of experiments was carried out in winter, i.e. during the resting period of the onions. In this respect it is noteworthy that according to MEYER (1957) the amount of free phosphatide acid in the plasma-membrane of onion cells is larger in the resting period. The London–van der Waals' forces and the Coulomb forces have therefore in this season entirely different values, and these differences will in their turn be responsible for differences in the way in which the permeability of the protoplasm is influenced by temperature.

§ 4. INFLUENCE OF CHLORIDES OF ALKALI METALS AND OF ALKALINE EARTH METALS ON THE PERMEATION RATE OF WATER

As in our experiments the salt concentrations were always low, and as there are no indications that salts penetrated into the protoplasm, the action sphere of the ions must have been restricted to the plasma-membrane. Under normal circumstances they exercise a stabilizing and regulatory influence on the latter. This is proved convincingly by the abnormal behaviour the protoplasts show in media in which no ions are present, and by the fact that in experiments in which the plasmolyte is diluted in different ways, the ratio between the concentrations of the various ions—within certain limits—proves to be of much greater importance than the absolute value of their concentration.

The results obtained with solutions in which the ratio between the concentrations of KCl and $CaCl_2$ varied, fully agree with what we might expect on account of Bungenberg de Jong's "complex theory".

The stability of the plasma-membrane is, according to this theory, partly determined by Coulomb forces. The cations exercise an important influence on the magnitude of the latter, but their influence on phosphatides differs from that on proteins. The ions that are adsorbed to the plasma-membrane may be exchanged against ions in the medium. This explains why it did not make much difference in our experiments whether deplasmolysis was obtained by lowering the concentration of the dextrose alone or by lowering that of the salts too (cf. Fig. 11).

The permeation rate appears to be strongly dependent on the ratiobetween the K- and Ca-salts in the medium (cf. Ch. III § 6). In the experiments undertaken to investigate the effect of various ratios of these salts, the sum of their concentrations was kept constant, and equaled 0.1 n. The results of these experiments are shown in Fig. 15. In this figure we see that KCl and $CaCl_2$ counteract to some extent each other's effect, and that this counter action is strongest, when the two salts are present in the same concentration (i.e. of 0.05 n).

An antagonism comparable to that observed in our experiments between the K- and Ca-ions, is seen, according to the investigations of Bungenberg de Jong, Booij and Wakkie (1936), only in phosphate colloids, but not in colloids of another type. In the phosphate colloids there is a definite ratio between the positive and the negative charges. Addition of salts changes this ratio, and in a membrane consisting of phosphatides this change must manifest itself in a change in permeability.

This enables us to understand the changes in permeability the plasma undergoes under the influence of solutions containing KCl and $CaCl_2$. When the concentration of each of the salts is 0.05 n, the mosaic formed by the distribution of the positive and negative charges will be such that the attraction between the phosphatide molecules reaches its highest value; this means that the permeability decreases to its lowest value. A change in the ratio between the salt concentrations causes an increase in permeability, and the latter will be larger when the KCl concentration is increased than when the Ca-concentration is increased. In the first case the Cl-ion will exercise a greater influence, because the antagonistic activity of the Ca-ions decreases. The K-ion alone is unable to maintain the charge mosaic of the phosphatide in the membrane. The mutual attraction of the membrane molecules accordingly decreases, and this causes the permeability to increase. When on the other hand the $CaCl_2$ concentration is increased and the KCl concentration simultaneously decreased, the charge mosaic in the phosphatide membrane also undergoes a change, but the latter is less marked than when the salt concentrations are changed in the opposite direction, and the increase in permeability too is less conspicuous. Soon a point is reached, at which the Ca-ions influence the distribution of the charges in the phosphatide component of the membrane in such a way that the attraction between the membrane molecules begins to increase, which causes a decrease of the permeability again.

In section 1 of this chapter the attention was drawn to the important work of TEUNISSEN (1936) and of TEUNISSEN and BUNGENBERG DE JONG (1938) on the influence of the salts of alkali metals and of alkaline earth metals on lecithin colloids. As in the present investigation the influence of salts of the same two groups of metals on the permeability for water has been investigated (cf. Table IX), we will try to find out in how far our results are in agreement with those of the Leyden school of colloid biochemistry. A study of the results obtained by Bungenberg de Jong *et al.* reveals that there is a rather considerable variability in the sequence of the ions when the latter are arranged according to the concentration that is required to obtain a reversion of the sign of the electric charge of lecithin-biocolloids. These differences in the sequence depend upon the kind of lecithin on which they acted. For the chlorides of the alkali metals the sequence nevertheless was always Li < Na < K. In our own experiments this same sequence was found when we compared the degree to which the metals of this group were able to decrease the permeability of the protoplasm: Li < Na < K. BOOIJ (1956) has once more drawn the attention to this sequence and to the fact that it applies only to the way in which they affect the phosphate colloids, as their influence on colloids with sulphate and carboxyl groups is just opposite. RAVEN *et al.* (1956) found in their study of the influence exercised by the salts of alkali metals on the mortality of *Limnaea stagnalis* a different sequence, viz. Li < K < Na. In our experiments the position of Cs just behind Li agrees well with that which it occupies in the sequence of these metals that was found in the study of the effect of their ions on the electrical charge of the egg lecithin; the position of Rb in our experiments, however, is anomalous, but this deviation from the expected sequence does not mean that the latter is of no importance. It should not be overlooked that the plasma-membrane contains besides lecithin other compounds, and that the latter may be affected by the salt mixture in a quite different way. Moreover, although the salt concentrations in our experiments were low, they were arbitrarily chosen; it is not impossible that the results would have shown complete agreement with the expectation if we could have studied a whole series of concentrations for each salt mixture; in that case we could have compared the mixtures with the optimal concentration. It is not even necessary that an ionic antagonism will show at every combination and concentration. The experiments of Raven that were quoted above, prove that it may be absent.

In the experiments with the chlorides of the alkaline earth metals the attempt to arrange the metal ions in a definite sequence met with more difficulties. With $MgCl_2$ no plasmolysis could be obtained, and the position of Mg could therefore not be ascertained. The results obtained with $BeCl_2$ should also be accepted with much reserve. It nevertheless seems justified to conclude that the sequence in which these metals should be arranged on account of the way in which their ions counteract the effect of the K-ion on the plasma-membrane, differs in a similar way as that which represents the action of their ions on lecithine colloids, from the Hofmeister sequence. Support for this conclusion is found in the circumstance that RAVEN (1957) observed a similar decrease from Be to Ca in the effect that these ions exercise on the mortality of *Limnaea*.

On account of these considerations it seems permissible to conclude that in the plasma-membrane of our onion gymnoplasts too lecithin colloids occupy a prominent position.

SUMMARY

1. LEVITT, SCARTH and GIBBS (1936) described a method for recording the osmotic behaviour of gymnoplasts, i.e. of protoplasts that, after plasmolysis, have been taken out of the cell wall; the record was obtained by photographing the gymnoplasts by means of a cinematographic camera attached to a microscope. This method was adopted by us, but instead of a single gymnoplast we photographed several at the same time.

2. The gymnoplasts we used, were isolated from the bulb scales of *Allium cepa* after plasmolysis in a solution containing 0.66 mol dextrose and varying concentrations of KCl and $CaCl_2$.

3. We studied the speed with which water passes into the gymnoplasts when the latter are partially deplasmolysed, and estimated the volume to which they expand on account of the partial deplasmolysis. The latter was obtained by diluting the plasmolyte either with pure water or with water in which KCl and $CaCl_2$ were dissolved in the same concentration as in the plasmolyte. We also studied the volume changes of gymnoplasts that were more than once plasmolysed and deplasmolysed.

4. It appeared that the degree of permeability, i.e. the speed with which water passes into the gymnoplasts, can be expressed clearly by means of the half-time constant, h.v.c. (cf. Ch. II, § 2).

5. As it is essential that the gymnoplasts we use for our experiments, are perfectly spherical, they were always controlled as to their shape. They appeared to deviate from the spherical shape only when there were no K- and Ca-ions in the medium (cf. Ch. II, § 1).

6. At a constant temperature, the volume of the gymnoplasts does not change, even when they remain for a considerable time in the plasmolyte. Therefore it is to be assumed that neither dextrose nor salts pass from the latter into the gymnoplasts. Only when the gymnoplasts, because of an unsuitable composition of the medium, are damaged, endosmosis or intrability of these solutes may take place.

7. If the gymnoplast behaved as an ideal osmotic system, it would obey van 't Hoff's law. In our experiments, however, small deviations were found, the change in volume remaining, as a rule, somewhat below the expected value (Ch. III, § 4). The cause of these deviations was discussed (Ch. IV, § 2 A).

8. The influence of temperature as well as that of the ratio between the concentration of the K-ions and that of the Ca-ions, on the speed with which water passes into the gymnoplast and on the magnitude of the volume the latter ultimately reaches, were experimentally investigated (Ch. III, §§ 2, 4 and 6).

9. Temperature proved to have a marked effect on the magnitude of the ultimate volume. A temperature of 2° C proved to be the only one at which the observed value agrees with the calculated one. At higher temperatures it always remains below the expected value, and at 20° C the difference between the observed value and the calculated one reached its highest value (Ch. IV, § 2 B). It was argued that these differences may be due to the influence temperature exercises, by the intermediary of the ATP system, on the sol-gel equilibrium in the protoplasm (Ch. IV, § 2 B).

10. The K- and Ca-ions in the medium too exercised a measurable influence on the ultimate volume. The observed value was always smaller than the expected one, and the largest deficit was found when the concentrations of the K-and Ca-ions

were equal (0.05 n). It was argued that it might be possible to explain this influence by assuming that in the plasma-membrane a charge mosaic is present, which would change under the influence of the K- and Ca-ions. The membrane potential would be lowest when the concentrations of the K- and Ca-ions are equal. Because of the membrane potentials that would arise when the concentrations of these ions are unequal, electro-endosmotic forces would come into action. The latter would be responsible for an increase of the amount of water that is absorbed, and this electro-endosmosis would, of course, increase with the membrane potential.

11. Within the range that was tested the ratio between the concentrations of the K- and Ca-ions was found to be of far greater importance than their absolute value.

12. The speed with which water passes into the gymnoplast, was found to be strongly dependent upon temperature. Up to the highest temperatures we could test, it was found to increase (Ch. III, § 2). The Q_{10} is considerably higher than that of an ideal osmotic process. Factors that might be responsible for this higher value, were discussed (Ch. IV, § 3).

13. K- and Ca-ions also influence the speed with which water passes into the gymnoplast. When they are present at the same time, they show a distinct antagonism, similar to that which appears in their effect on phosphate colloids. The speed with which water passes into the gymnoplast, reaches its lowest value when the concentrations of the K- and Ca-ions are equal (0.05 n). The effect of an increase in the concentration of the K-ions accompanied by an equivalent decrease of the concentration of the Ca-ions, appears to be greater than that of a corresponding increase in the concentration of the Ca-ions accompanied by a similar decrease in the concentration of the K-ions. These facts form a strong argument in favour of the view that phosphate colloids (lecithin) play an important part in the composition of the plasma-membrane (BUNGENBERG DE JONG *et al.*, 1936–1957, cf. Ch. IV, § 4).

14. The view that phosphate colloids, and especially lecithins, are an important constituent of the plasma-membrane, finds support in the results of some preliminary experiments on the effect which other uni- and bivalent ions exercise on the speed with which water passes into the gymnoplasts. When the univalent ions are arranged according to the degree in which equal concentrations of them increase the resistance of the plasma-membrane against the passage of water, we obtain the sequence $Rb < Li \leqslant Cs < Na < K$, which agrees completely with that which TEUNISSEN (1936) and TEUNISSEN and BUNGENBERG DE JONG (1938) found when they determined the concentrations of univalent cations that are required for reversing the electric charge of lecithin. The noxious influence of Mg- and Be-ions made it difficult to work out a similar sequence for the bivalent ions, but it probably is Be (?) < Mg (?) < Ba < Sr < Ca.

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LIGHT-DEPENDENT CHLORIDE ABSORPTION IN VALLISNERIA LEAVES

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CHAPTER 1

INTRODUCTION

The origin of this investigation lies in the phenomenon studied by Arisz *et al.* (1943, 1947) that light enhances the absorption of chloride in Vallisneria leaves, and that this light influence does not depend on the presence of carbon dioxide in the medium. The present investigation was carried out with the purpose to gain a better insight into this influence of light on chloride absorption.

The main result was the finding that Vallisneria leaves are capable of utilising the energy of light absorbed in the chloroplasts as a source of the energy required in chloride absorption as well as in photosynthetic carbon assimilation. Furthermore, it was found that in the light, under conditions largely preventing cytochrome oxidase activity chloride absorption is by no means abolished, which proves that chloride absorption in Vallisneria leaves needs not necessarily be coupled with respiration as far as this process is mediated by cytochrome oxidase.

A stimulation of salt absorption by light was found earlier in a number of organisms: in *Elodea canadensis, Ceratophyllum demersum, Myriophyllum* spec.: Ingold (1936), and in *Nitella clavata:* Hoagland *et al.* (1924, 1927). In none of these cases, however, carbon dioxide was excluded from the medium. It is therefore not impossible that the whole effect of light in these cases was due to photosynthetic carbohydrate formation. The stimulation of potassium absorption from seawater in *Valonia macrophysa* by light, found by JACQUES and OSTERHOUT (1934), was ascribed by the authors to the increase in the pH of the medium caused by photosynthesis. SCOTT and HAYWARD (1954) found that in the light *Ulva lactuca* excretes sodium ions. This process according to the authors is not inhibited by substances which inhibit photosynthetic carbon assimilation. Presumably, therefore, in this case there is a more direct influence of light on the process, similar to what was found with Vallisneria. In none of these investigations the salt absorption was studied in light of varying wavelengths. There is, therefore, no convincing evidence that in any of these cases chlorophyll absorbed the light active in salt absorption, as was found in the experiments with Vallisneria reported here.

According to KESSLER (1955) the reduction of nitrate in *Scenedesmus* is greatly stimulated by light in the absence of carbon dioxide. Also, BONGERS (1956) found that in normal *Chlorella* cells nitrate reduction occurs in the light only; the process competes with carbon dioxide reduction for reducing power generated in the chloroplasts. Perhaps these processes too have something in common with the light-dependent chloride absorption in Vallisneria leaves.

In the following a survey of the contents of the paper is given.

A description of material and methods (Chapter 2) is followed by a Chapter (3) on the velocity with which chloride absorption in Vallisneria leaves responds to exposure to light. The reaction to light was found to be quite rapid: it took about five minutes before the absorption rate was maximal.

In the next Chapter (4) the action spectrum will be treated, a subject discussed more fully in an earlier paper: VAN LOOKEREN CAMPAGNE (1957). From the action spectrum it was concluded that the light active in chloride absorption is absorbed by chlorophyll. This pointed to a more or less close connection between photosynthesis and chloride absorption.

Therefore, in Chapter 5 the reciprocal interaction between carbon assimilation and chloride absorption was studied. In agreement with Arisz's earlier findings the presence of carbon dioxide had no influence on chloride absorption, but bicarbonate ions had an inhibiting effect. Chloride had no effect on either carbon dioxide or bicarbonate assimilation. These data were thought to indicate that carbon assimilation products or intermediates are not involved in the chloride absorption process.

Consequently the energy required in chloride absorption must be supplied and utilised in another form. By means of inhibitors an attempt was made to get some indications as to the form of metabolic energy involved. Carbon monoxide (Chapter 6) and cyanide (Chapter 8) yielded data liable to more than trivial interpretation, as did oxygen withdrawal (Chapter 7).

The other inhibitors tested were hydroxylamine, 8-hydroxyquinoline, fluoride, azide, 2,4-dinitrophenol, arsenate, arsenite, mono-iodo-acetate, phenylmercuri-nitrate, ethylenediaminetetraacetate.

These substances apparently caused reversible or irreversible changes in the cytoplasm and did not show any evidence of a more specific influence on the chloride absorption mechanism. They were, therefore, unsuitable for the purpose outlined above.

The inhibition of chloride absorption by bicarbonate finally, gave rise to some observations concerning the photosynthetic assimilation of bicarbonate as compared to carbon dioxide assimilation (Chapter 9). This chapter also contains a rectification of an earlier paper in which it was stated that there is no photosynthetic assimilation of bicarbonate in Vallisneria leaves: VAN LOOKEREN CAMPAGNE (1955).

The implications of the experimental data are discussed in Chapter 10 in connection with data from literature.

CHAPTER 2

MATERIAL AND GENERAL METHODS

Plants of *Vallisneria spiralis* L. (*Hydrocharitaceae*) were grown in concrete culture basins which were about 50 cm deep, were filled with deionised water and contained a 10 cm bottom layer of clay rich in organic matter. They were artificially illuminated during 15 hours daily with about 2800 meter-candles light from Philips HO 450 watt mercury vapour lamps; the temperature was 20–25° C.

Leaves to be used in an experiment were selected for healthy appearance and complete absence of injuries, and cut into 4 × 50 mm strips. The leaf strips were arranged into sets of eight (about 500 mgm fresh weight), and inserted into perspex frames which fitted in the experimental vessels described later on. They were kept overnight in the dark in water from the culture basin; after his treatment wound effects have largely disappeared: ARISZ (1957 I).

All photosynthesis experiments were carried out in a 17.5 ml closed perspex vessel containing eight leaf strips mounted in a perspex frame (Fig. 1). During the experiments the vessel was placed in a water bath at 24° C. The contents were stirred by turning the vessel back and forth by a mechanical device.

In the earlier experiments the oxygen content of the solution was determined before and after photosynthesis had taken place according to the micro-Winkler method: VAN DAM (1936), VAN LOOKEREN CAMPAGNE (1955). Later on a simple volumetric method was developed yielding results of the same accuracy, and permitting the time course of oxygen evolution to be followed. To this end a capillary calibrated glass tube was attached to the lower outlet tube of the vessel (Fig. 2). The upper outlet tube was closed after filling the apparatus with the experimental solution up to the capillary tube, leaving about 2 ml of air in the vessel.

Volume changes of the air space in the vessel can be read from the calibrated capillary tube. The hydrostatic pressure inside the vessel has to be kept constant in order to prevent a. variations in the total gas pressure in the vessel, b. variations in the total volume of the vessel itself, perspex being rather flexible, c. variations in the volume of the piece of bicycle valve rubber tubing which connects the vessel to the calibrated glass tube. To this end the liquid meniscus in the calibrated tube is kept at a constant distance above the water level of the constant temperature bath in which the vessel is immersed. This is done by lowering the calibrated tube over the same distance over which the meniscus had risen in the calibrated tube.

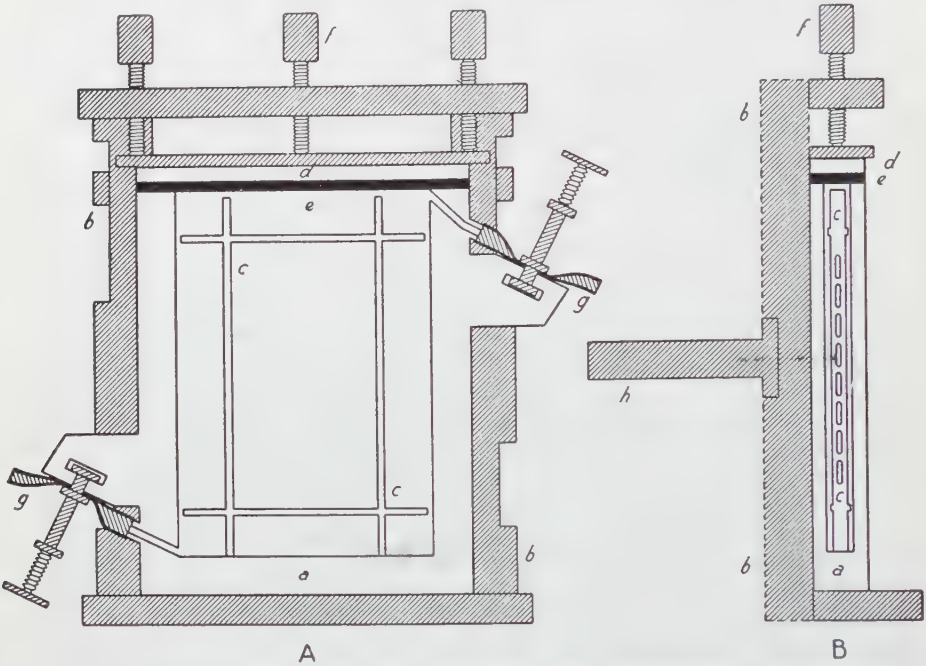

Fig. 1. Closed perspex vessel for absorption and photosynthesis experiments. Internal dimensions 8 × 50 × 80 mm. A. Front view; B. Longitudinal section. The perspex vessel a. is mounted in a brass frame b. The perspex holder c. with the leaf strips (not shown) is placed in the vessel. The vessel is sealed by a lid d. provided with a rubber strip e. and pressed firmly on the vessel by means of the screws f. Filling and emptying the vessel are accomplished by means of the rubber tubes g., which can be closed by means of screw clamps. By means of the axis h. the frame b. is placed in a shaking device which is inserted into the constant-temperature bath. By this device the vessel is turned back and forth in the plane perpendicular to the axis h.
(From van Lookeren Campagne 1955)

The apparatus thus constitutes a volumetric device with an uncompensated manometer, which at the same time serves as a volumeter. From the volume changes recorded at constant total gas pressure the oxygen production can be calculated according to an appropriate equation. In this equation the fact should be taken into account that all gases present are to some extent dissolved in the liquid phase, and that the amounts dissolved are directly proportional to the partial pressures of the gases concerned. This is necessary because the volume of the liquid phase is about 7.5 times as large as the gas phase. In literature (Warburg and Negelein, and Dixon, quoted in Umbreit *et al.* (1949); Cunningham and Kirk, quoted in Glick (1949); Yocum and Blinks (1954); Kok (1955) no equation was found which met this requirement.

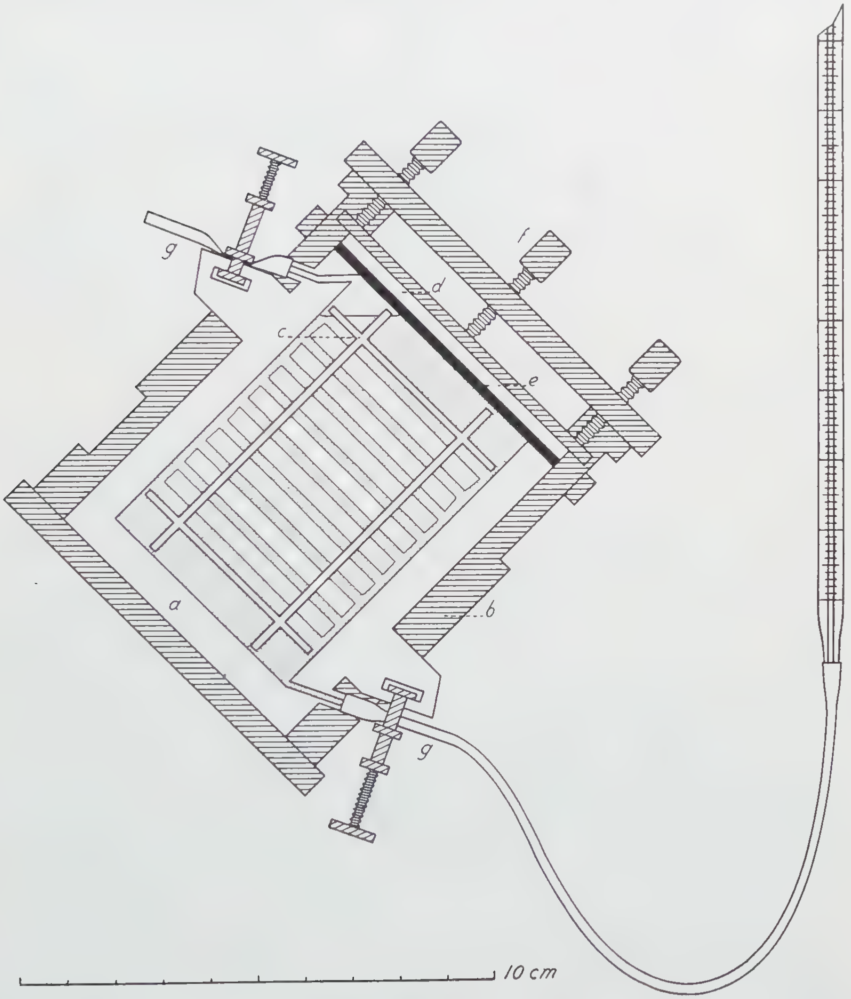

Fig. 2. Arrangement for volumetric oxygen determination. The calibrated capillary glass tube is connected to the lower outlet tube of the vessel containing the leaf strips. The experimental solution, which fills the vessel for the greater part, also serves as an indicator liquid in the calibrated tube. For explanation of the letters see Fig. 1.

Therefore an equation was derived as described in the Appendix, which gives the ratio of oxygen produced to volume change recorded at constant total gas pressure. Under the conditions of the experiments this quotient was according to calculation surprisingly insensitive to variations in the values of the determining factors such as solubility coefficients and partial pressures of the gases, or the gas-to-liquid volume ratio. Errors due to variations in atmospheric pressure and thermostat temperature were negligible: if the gas phase was 2 ml 1 millibar atmospheric pressure change corresponded to about 2.5 μl volume change recorded, and 1° C. temperature change corresponded to about 16 μl volume change recorded. Temperature equilibration took about 15 minutes. The error in the determinations was about 2 μl, or 0.1 μmol oxygen.

Gas exchange between liquid phase and gas phase was promoted by turning the vessel back and forth as said above. The equilibration time was determined mainly by the velocity of gas exchange between the gas spaces within the leaf strips (amounting to about 30 vol%) and the medium; this process can not be sped up by stirring the medium. The time course of equilibration was determined by following the gas volume in the apparatus after part of the gases had been removed from the leaves by pretreatment with air-free water (Fig. 3). The time of half equilibration as estimated from the figure was about 20 minutes.

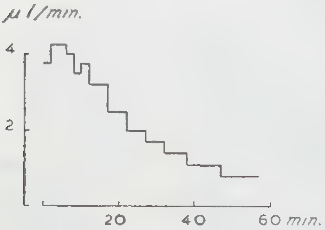

Fig. 3. Time course of gas equilibration between the gas spaces in the Vallisneria leaf strips and the air bubble in the vessel. Volume change in the vessel was recorded as a function of time after partial evacuation of the gas spaces in the leaf strips.

Strongly reduced pressure in the gas spaces does not cause infiltration of liquid into the leaves because the gas spaces are divided into compartments by perforated septa: Solereder (1913, p. 63) which permit rapid passage of gases but keep water outside like tiny umbrellas as long as the leaf tissue is in good condition.

The conditions in the experiment of Fig. 3 are not entirely comparable to those prevailing during the photosynthesis experiments, because in the latter case, broadly speaking, only oxygen is involved in the gas exchange, whereas in the former case air, i.e. mainly nitrogen was involved. As the solubility of oxygen is twice the solubility of nitrogen in water, and the diffusion velocity of both gases in water is approximately equal the equilibration time for oxygen alone is probably appreciably shorter than for air. This obtains only of course when the gas solubility and the diffusion velocity in Vallisneria leaf tissue are about the same as in water, which is to be expected: Krogh (1919).

The chloride absorption experiments were mostly carried out in four vessels of the type shown in Fig. 4. These vessels were filled from a 25 ml pipette; stirring was provided by aeration. The method was established by Arisz (1956).

In most experiments the solution was 5×10^{-4} M KCl, to which 2.5×10^{-4} M $CaSO_4$ was added in order to prevent injury by a single salt solution. Other substances were added separately as required.

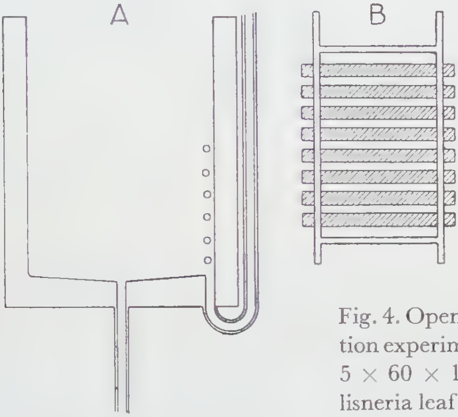

Fig. 4. Open perspex vessel for chloride absorption experiments. A. Vessel. Internal dimensions $5 \times 60 \times 100$ mm; B. Perspex frame with Vallisneria leaf strips.

Passive diffusion of chloride ions into or out of the leaf strips was not found to occur to a measurable extent in the experiments described here, owing to the low chloride concentrations used. Arisz found that no measurable quantity of chloride can be washed out of Vallisneria leaves following incubation in a chloride solution: Arisz (1954), Arisz and Sol (1956, p. 242).[1]

Titration was carried out electrometrically with 0.01 M $AgNo_3$: Piper (1944); total chloride in the medium was determined after absorption had taken place. The difference with blank determinations yielded the chloride absorption. The error in the absorption data was not more than 0.1 μmoles chloride, as compared to absorption values of 1 to 2 μmoles chloride per hour. The reference quantity was eight leaf strips (about 500 mgm fresh weight).

The absorption experiments consisted in a series of one-hour periods; as a rule standard treatments alternated with other treatments. This was necessary because the absorption rate does not remain constant in the course of the experiments (Sol, personal communication). Before the first absorption period the leaf strips were always exposed to light in the experimental chloride solution during about 45 minutes. This was done because during this time the chloride absorption rate is often much lower than later on.

As said above the leaf strips were kept overnight in the dark in water from the culture basin before they were used in an experiment. Following this pretreatment in the dark the chloride absorption rate is in most cases relatively steady, whereas following pretreatment in the light the chloride absorption rate often strongly decreases with time (SOL, personal communication).

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[1] The apparent free space in Vallisneria leaves was found to be 4%: A. Kylin, Physiol. Plant. *10*: 732 (1957) (note added in proof)

The light source used in most experiments was a Philips SO 140 watt sodium vapour lamp. Light intensity was measured with a General Electric selenium-cell photometer reading in foot-candles. In the case of coloured light ¹) the intensity was recalculated in ergs cm $^{-2}$ sec $^{-1}$; to this end the photometer was compared to a Kipp small area thermopile. The exact calibration value of the thermopile was unknown; in the calculations the approximate calibration value given by the factory, 0.16 μvolt per μwatt was used.

Special techniques will be described together with the experiments in which they were used.

CHAPTER 3

TIME COURSE OF LIGHT-INDUCED CHLORIDE ABSORPTION

It was thought that the velocity with which the chloride absorption responds to changes in illumination would possibly yield some indication as to the way in which light influences chloride absorption. Therefore the time course of chloride absorption at light-dark transitions was followed by continually measuring the electric conductivity of the medium. The same technique was used by LUNDEGÅRDH (1949). The experimental arrangement is shown in Fig. 5. A 4 × 100 mm leaf strip was inserted into a slot-shaped perspex vessel measuring 1 × 4.2 × 120 mm. Subsequently the vessel was closed and immersed into a water bath at 24° C. About 1.5 ml of a 2×10^{-4} M potassium chloride solution was pipetted into the apparatus. The solution was circulated by means of air bubbles as shown in Fig. 5. This resulted in a rapid mixing: within one minute all concentration differences were levelled out. Conductivity was determined at two minutes' intervals by means of a Philips Philoscop GM 4140 connected to two platinum wire electrodes. The measuring current was generated by a Philips low-frequency oscillator GM 4260 at 2 Volts and 1000 cycles/sec. Conductivity change (arbitrary units) was used as a measure of chloride absorption.

A typical experiment is shown in Fig. 6.

It can be seen that light-induced chloride absorption starts abruptly some five minutes after the light is turned on; when the light is turned off the absorption stops almost immediately. This rapid response indicates that light has a direct effect on the chloride absorption process proper and not on membrane permeability. The lag period is not perceptibly dependent on light intensity. As shown in Fig. 24 (Chapter 9) photosynthesis behaves in essentially the same way during the induction period. It seems, therefore, as if carbon dioxide fixation and light-induced chloride absorption are during the

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¹) In preliminary experiments by Mr J. H. Mook a Christiansen light filter was used, which was kindly procured by Kema (Arnhem).

induction period limited by a common process. This is not unreasonable as in both processes the light is absorbed by the chlorophyll system (Chapter 4). The point will be treated in the Discussion (Chapter 10).

The experiment in Fig. 6 clearly shows that the accuracy of the conductivity measurements is too low to permit usable quantitative determinations of the chloride absorption to be made. In all subsequent experiments chloride absorption was, therefore, determined by titration of the medium after one-hour absorption periods as already described. From Fig. 6 it is also clear that the induction

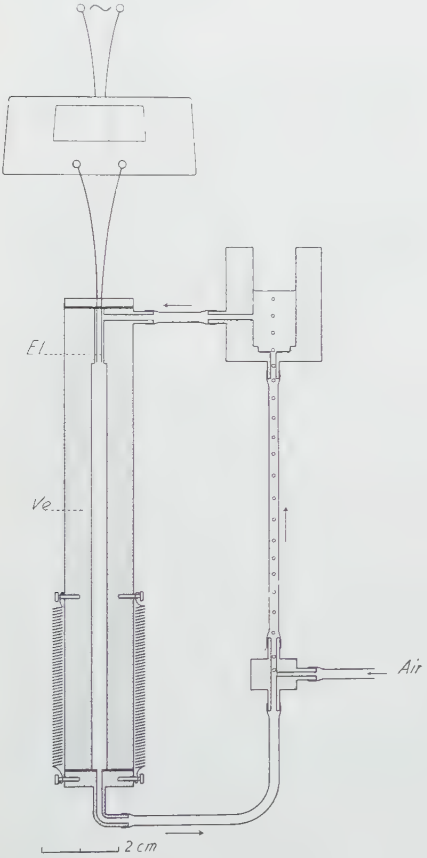


Fig. 5. Arrangement for determination of electric conductivity in the medium during chloride absorption. Vessel Ve (internal dimensions 1 × 4.2 × 100 mm) with a 4 × 100 mm Vallisneria leaf strip and two platinum wire electrodes El which are connected to a Philips Philoscop resistance meter (measuring current 1,000 cycles/sec. a.c.); circulation of the medium (1.5 ml) effected by ascending air bubbles.

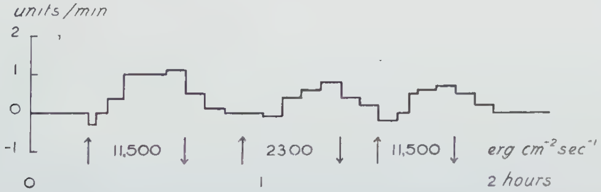


Fig. 6. Time course of light-induced chloride absorption in Vallisneria leaves. 2×10^{-4} M KCl + 10^{-4} M $CaSO_4$; sodium light; 24° C. (↑ light on; ↓ light off).

period is too short to influence the measurement of steady-state chloride absorption seriously if the absorption period is at least one hour.

CHAPTER 4

LIGHT CURVE AND ACTION SPECTRUM

These subjects were treated in detail in an earlier paper: VAN LOOKEREN CAMPAGNE (1957). A brief survey of the results will be given here.

The light curve of the chloride absorption was determined mainly in order to know the range in which the light intensity limits chloride absorption. This was necessary as an action spectrum can only be determined in the range of rate-limiting light intensities.

The light curve was determined in experiments in which one-hour periods with a standard light intensity alternated with one-hour periods in which other light intensities were used. This made it possible to calculate relative absorption values, which are less variable than the absolute absorption values. The sodium vapour lamp was used as light source.

The result is given in Fig. 7 (A). At 4500 ergs cm^{-2} sec^{-1} sodium light saturation was reached. Below this intensity the chloride absorption was more or less rectilinearly proportional to the light intensity. It should be noted that in the dark too there is some

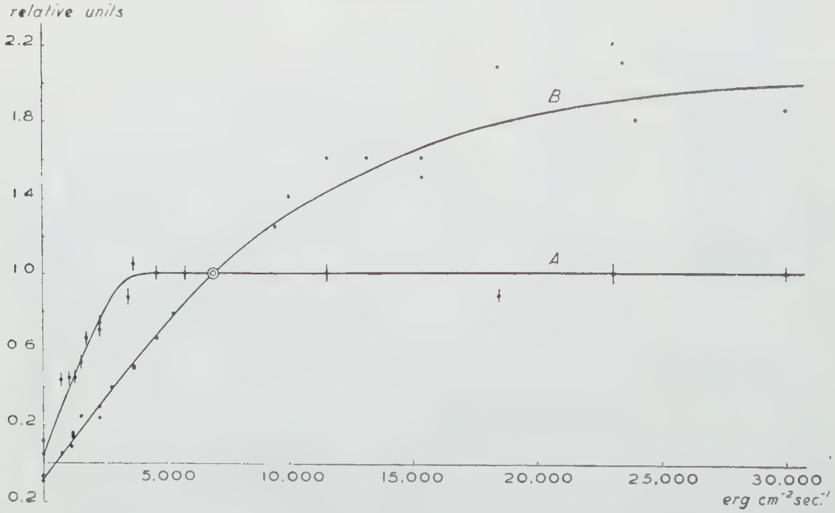


Fig. 7. Light curve of chloride absorption (A) and of photosynthesis (B) in Vallisneria leaves. Chloride absorption from 10^{-3} M KCl + 2.5 × 10^{-4} M $CaSO_4$; photosynthesis from 10^{-3} M CO_2 + 10^{-3} M $KHCO_3$ + 2.5 × 10^{-4} M $CaSO_4$; 24° C. Reference light intensity 7.000 ergs cm^{-2} sec^{-1} sodium light. (Partly from van Lookeren Campagne 1957)

chloride absorption. This absorption in the dark may be appreciably higher in other experiments (Figs. 11, 14, 15). The light intensity at which light saturation is reached is not always the same: it may shift in the course of weeks or months. Mr. J. H. Mook, using non-monochromatic light obtained with Schott filters, found similar curves (unpublished).

For comparison the light curve of photosynthesis, also shown in Fig. 7 (B), was determined in an analogous manner using the micro-Winkler method of oxygen determination. Light saturation is reached at a much higher intensity, about six times as high as required for the saturation of chloride absorption. The implications of this fact will be treated in the Discussion (Chapter 10).

The maximum rate of chloride absorption was found to be independent of the wavelength of the light used (experiment not shown).

The action spectrum of a light-dependent process is the curve in which the effect of a constant light intensity (in quantum units) is plotted against the wavelength of the light. If we assume that the effect of each quantum, once it is absorbed, is independent of the wavelength, the action spectrum represents the absorption spectrum of the pigment involved. The absorption spectrum and consequently the action spectrum can yield useful information on the chemical identity of this pigment. The principle was found by Warburg, who applied it in the identification of cytochrome oxidase as an iron porphyrin compound.

In order to establish the action spectrum the chloride absorption was determined at various wavelengths using equivalent light intensities: i.e. intensities causing the same rate of absorption, as determined in preliminary experiments.

Standard treatments alternated with other treatments in the successive experimental periods, as described in Chapter 2. Standard treatment in this case was exposure to a constant light intensity at wavelength 589 mμ. This wavelength was used as the reference wavelength. Light of the desired wavelengths was obtained by means of interference filters with about 10 mμ half-peak width, type Filtraflex B manufactured by Gerätebauanstalt Balzers (Liechtenstein). Schott filters were not sufficiently selective; with the Christiansen filter the highest intensities obtainable were not high enough. In each experiment a control period was included during which a higher light intensity was used to make sure that during the other periods the light intensity had actually been limiting the chloride absorption.

The intensities which caused identical chloride absorption rates were calculated in relative quantum units, the intensity at 589 mμ being put equal to unity. The reciprocals of these values are a measure of the efficiency with which light is utilised in chloride absorption. In Fig. 8 (A) these reciprocals are plotted as a function of a wavelength, thus yielding the action spectrum.

For comparison the same procedure was followed to establish the action spectrum of photosynthesis. The curve found coincided exactly with the action spectrum of chloride absorption. This proves that the chlorophyll system absorbs the light effective in the induction of chloride absorption by Vallisneria leaves.

As a further confirmation of this conclusion the light transmission of a Vallisneria leaf was determined (Fig. 8 (B)). No correction for scattering was applied.

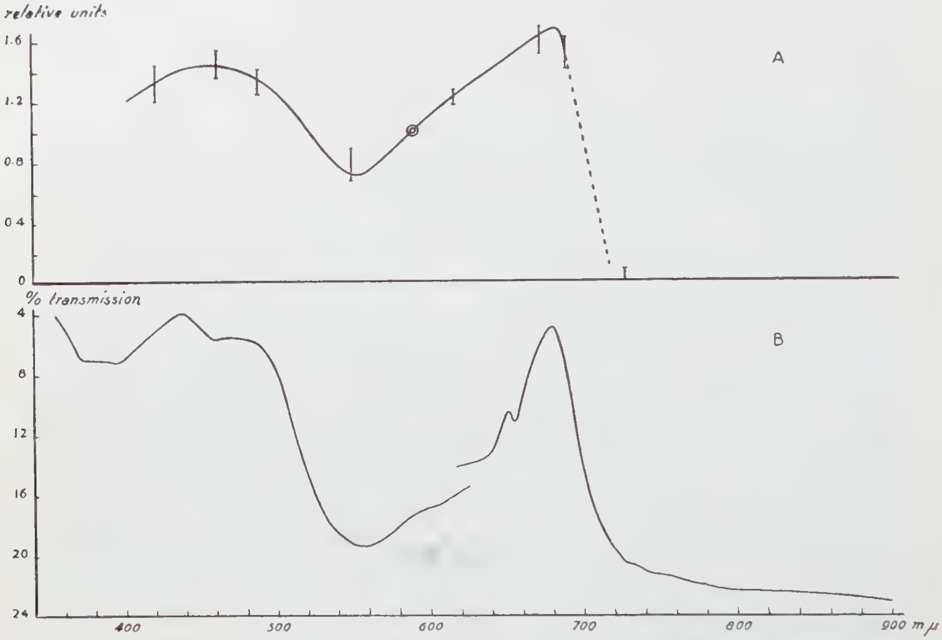


Fig. 8. A. Action spectra of chloride absorption and photosynthesis in Vallisneria leaves. Reference wavelength 589 mμ. Variation of calculated values indicated by the vertical lines. B. Transmission spectrum of a water-logged leaf of Vallisneria. No correction was applied for scattering. (From van Lookeren Campagne 1957)

It should be mentioned here that essentially no carbon dioxide was present in the vessel during chloride absorption. This suggests that carbon dioxide assimilation is in no way involved in the chloride absorption process. More evidence for this supposition will be given in the next chapter.

CHAPTER 5

CHLORIDE ABSORPTION AND PHOTOSYNTHETIC CARBON ASSIMILATION

As shown in the previous chapter chlorophyll is involved in light-induced chloride absorption. When this was found the first question was, of course, whether there is a direct interaction between photosynthetic carbon assimilation and light-induced chloride absorption. So it was tried to find out if the presence of carbon dioxide had any influence on the rate of chloride absorption. This attempt met with a complication: in preliminary experiments more than once results were obtained which suggested that at a pH lower than 5.5, especially in media buffered with phosphate, chloride absorption was depressed. Therefore, it was thought better to prevent the occurrence of low pH values in the medium. Consequently when the medium was aerated with air containing more than a trace of carbon dioxide bicarbonate was added to the medium in order to raise the pH to above 6 or higher. If now, as was really found, under these conditions the chloride absorption is diminished the problem presents itself whether this inhibition is caused by the presence of carbon dioxide molecules or the presence of bicarbonate ions.

It was attempted to solve this problem by comparing the influence of varying the carbon dioxide concentration while the potassium bicarbonate concentration was kept constant, and vice versa. Experiments carried out according to this principle met with two difficulties: Firstly, it was found that the bicarbonate concentration did not remain constant during a one-hour absorption period: depending on the pH the leaf strips presumably exchanged hydrogen ions against other cations, or vice versa, thereby converting bicarbonate into carbon dioxide or vice versa. This process becomes troublesome at bicarbonate concentrations from 10^{-3} M downward.

Secondly no equilibrium with regard to carbon dioxide concentration existed between the solution in the vessels and the gas bubbling through. The carbon dioxide concentration actually established in the medium depended on the light intensity, i.e. the rate of photosynthesis, as was tentatively concluded from the pH value of the medium at the end of the absorption periods.

These facts must be borne in mind when the results of the experiments are considered. Examples are shown in Figs. 9, 10, 11. The final bicarbonate concentrations given in the figures should be considered as approximate values; they were calculated from the pH, determined with a glass electrode, and from the estimated carbon dioxide concentration.

From Fig. 9 it may be seen that at low concentrations of both carbon dioxide and bicarbonate there is no inhibition of chloride absorption at all.

In Fig. 10 an experiment is given showing that at a constant carbon dioxide concentration bicarbonate ions at the higher concentrations

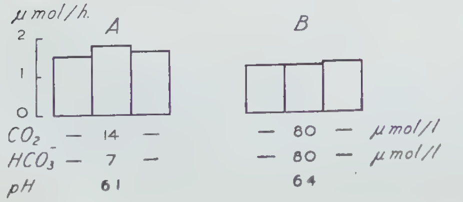


Fig. 9. Chloride absorption in the presence of carbon dioxide and bicarbonate at low concentrations. 5×10^{-4} M KCl $+ 2.5^{-4}$ $MCaSO_4$; 24° C.; 4500 ergs cm^{-2} sec^{-1} sodium light; pH values mentioned are final pH values.

have a markedly inhibiting influence on chloride absorption, in the light as well as in the dark. Phosphate and nitrate, to the contrary, have but a slight, or no effect, Sol (unpublished).

No attempt was made to establish the quantitative relationship between the bicarbonate concentration and the inhibition of chloride absorption, because the inhibitions observed were too variable.

Olsen (1953) and Steward and Preston (1941) also found a specific inhibitory effect of bicarbonate on salt absorption.

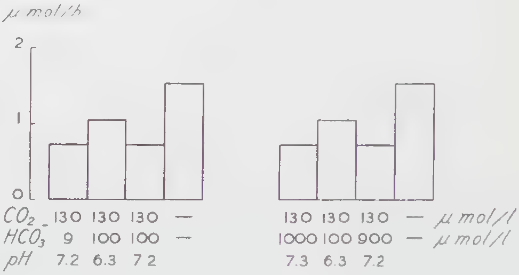


Fig. 10. Chloride absorption at constant carbon dioxide concentration and varied bicarbonate concentration. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; sodium light; pH values mentioned are final pH values.

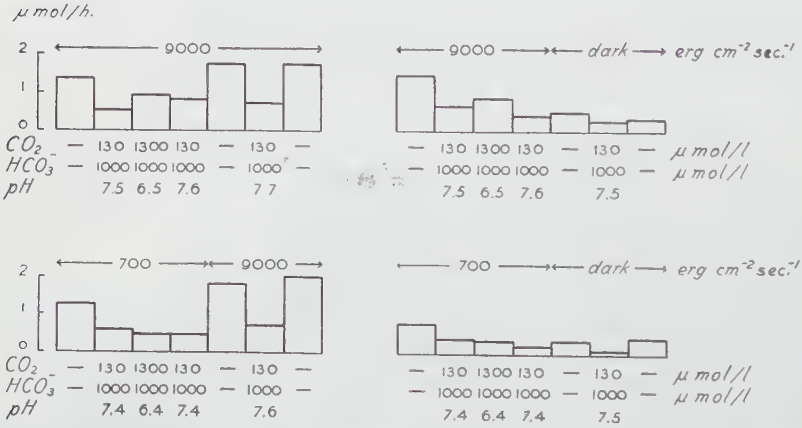


Fig. 11. Chloride absorption at constant bicarbonate concentration and varied carbon dioxide concentration. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; sodium light; pH values mentioned are final pH values.

Carbon dioxide, on the other hand, has but little influence (Fig. 11), even at high carbon dioxide concentration and limiting light intensity (700 ergs cm^{-2} sec^{-1}): at the lower light intensity it appears to inhibit somewhat, at the higher intensity (9000 ergs cm^{-2} sec^{-1}) it slightly stimulates chloride absorption. Perhaps there is some competition between chloride absorption and carbon dioxide reduction at the limiting light intensity, whereas at the higher light intensity the respiration-dependent chloride absorption is possibly stimulated somewhat by products or intermediates of photosynthesis (cf. Discussion).

In any case it is clear that carbon dioxide reduction cannot be very directly involved in any part of the chloride absorption process. It is supposed, therefore, that after being transformed into chemical energy in the chloroplasts, the light energy is not utilised in the chloride absorption process as a carbon dioxide reduction product or intermediate, at least not to any appreciable extent.

In order to obtain some evidence as to the mechanism of the inhibition of chloride absorption by bicarbonate ions it was tried whether chloride ions also inhibited photosynthetic bicarbonate assimilation, a process discussed in Chapter 9. In the experiments carried out to this end the utilisation of bicarbonate was determined by measuring the pH before and after a 7 hours' period of incubation with a Vallisneria leaf piece.

Each of a series of test tubes was provided with 20 ml of a 3×10^{-3} M potassium bicarbonate solution to which either no, or 6×10^{-3} M, or 3×10^{-2} M potassium chloride was added, a 10 cm piece of Vallisneria leaf being subsequently introduced into each, some blanks excepted. The test tubes were well closed during the experiments. pH was measured with a Beckman type H pH meter. To this end the solution from each test tube in turn was transferred to a small beaker and after the measurement was poured back into the test tube.

From the pH the ratio of carbonate to bicarbonate concentration could be calculated according to the equation $\frac{CO_3^= \times H^+}{HCO_3^-} = K_2 = 10^{-10.3}$. As the initial bicarbonate and carbonate concentrations were known it was possible to calculate the final carbonate concentrations with the assumption that the cation concentration remained unaltered. The calculated increase in carbonate was taken as a measure of bicarbonate utilisation. The results of the experiment are shown in Table I. At the lower concentration chloride has no detectable effect on bicarbonate utilisation; at the higher concentration chloride has an apparently depressing effect, but here the pH measurement is not entirely reliable as a consequence of the high salt concentration. Possibly the effect, if it is real at all, is of merely osmotic nature, and not specific for chloride, cf. ARISZ and SOL (1956); ARISZ and SCHREUDER (1956 II). At any rate there is no convincing evidence that chloride ions interfere with photosynthetic bicarbonate utilisation.

Mutual interference between chloride ions and bicarbonate ions at a carrier somewhere at the outer boundary of the cytoplasm cannot be, therefore, the cause of the inhibition of chloride absorption by bicarbonate, but an interaction situated at the tonoplast, for instance, is quite possible, as in that case no influence of chloride on bicarbonate utilisation in the chloroplasts could possibly be expected, even if there is competition.

The inhibition of light-induced chloride absorption cannot lie in an enzyme system it has in common with photosynthesis, because photosynthesis has never been found to be impaired in the presence of bicarbonate.

TABLE I

Influence of chloride on bicarbonate utilisation in photosynthesis. Medium 20 ml $KHCO_3$ 3 × 10^{-3} M + $CaSO_4$ 5 × 10^{-5} M incubated for 7 hours, with a leaf piece 10 cm long. Light intensity 16,000 ergs cm^{-2} sec^{-1} sodium light. Temperature 24° C.

KCl, M		—						6 × 10^{-3}					3 × 10^{-2}					
pH	initial	9.4^3	9.3^8	9.4^0	9.4^1	9.4^1	9.4^1	9.3^7	9.3^7	9.3^6	9.4^0	9.3^8	9.2^2	9.2^1	9.2^1	9.2^0	9.2^2	9.2^0
	final	9.4^3	10.1^8	9.9^2	9.9^4	9.8^7	10.0^3	9.9^9	9.9^1	9.7^4	10.0^0	10.0^0	9.5^7	9.6^6	9.5^8	9.5^4	9.7^2	9.2^0
CO_3, μ moles	initial	6.3						6.6					6.3					
	final	18.0	13.5	14.1	12.6	15.6		15.6	14.1	11.4	15.6	15.6	11.1	12.3	11.4	10.8	13.5	
$\triangle CO_3$, μ moles		11.7	7.2	7.8	6.3	9.3		9.3	7.8	5.1	9.0	9.3	4.8	6.0	5.1	4.5	7.2	
leaf width, mm.		8^5	7	6^5	6	7		8	6^5	5^5	8	7^5	7^5	7^5	6	6^5	6	
$\triangle CO_3$, μ moles/h × 16 cm^2		3.2	2.4	2.7	2.4	3.1		2.7	2.7	2.1	2.6	2.9	1.5	1.9	2.0	1.6	2.8	
mean ± standard deviation of the mean		2.8 ± 0.2						2.4 ± 0.2					2.0 ± 0.3					

The phenomenon reminds one of the inhibition by bicarbonate of the respiration of plant roots studied by MILLER and THORNE (1956). There is a difference: the chloride absorption in Vallisneria is rapidly inhibited without time lag, whereas the respiration of root tips is not inhibited during the first hour in a medium containing bicarbonate. The difference is not necessarily essential because the time lag with root tips is probably caused by slow penetration of bicarbonate: in extracts of root tips the oxidation of cytochrome c is inhibited at the moment bicarbonate is added: MILLER and EVANS (1956). These authors suppose that the inhibition of respiration in roots is caused by an inhibition of cytochrome oxidase, but it is not clear whether they mean by the term "cytochrome oxidase" the terminal oxidase only or the whole enzyme system involved in the oxidation of cytochrome c. At any rate the site of inhibition can be anywhere between cytochrome c and oxygen in the respiratory reaction chain.

An influence of chloride in the medium on carbon dioxide assimilation was not found. It could, indeed, hardly be expected as even bicarbonate assimilation is not affected by chloride.

CHAPTER 6

INFLUENCE OF CARBON MONOXIDE

Several authors have shown that "active" salt absorption in plants is strongly inhibited by carbon monoxide: ORDIN and JACOBSON (1955), MIDDLETON (1955), SUTTER (1950), WEEKS and ROBERTSON (1950). They always used nonphotosynthetic organs or tissues, in which active salt absorption is necessarily dependent on the only available source of metabolic energy, *viz.* the respiration. Consequently, when carbon monoxide brings the respiration to a stand-still by blocking the ultimate oxidase there is no more respiratory energy available, and salt absorption must necessarily also come to a stand-still.

With photosynthetic cells and tissues the situation is different. Here, metabolic energy can be derived from light energy in the chloroplasts. In the present study it has already been demonstrated that Vallisneria leaves can utilise energy derived from light in chloride absorption.

As GAFFRON (1935) proved that steady-state photosynthesis is not inhibited by carbon monoxide the conversion of light energy into metabolic energy is evidently not influenced by carbon monoxide. So it should be possible to check whether the chloride absorption process proper is inhibited, and consequently whether autoxidisable heavy-metal compounds play a part in this process.

KRALL (1955) and GAFFRON (1935) found an inhibition of photosynthesis during an induction period after a pretreatment in the dark with carbon monoxide. According to the authors the effect was completely the same as that obtained with anaerobic pretreatment in the dark. It does not prove the indispensability of a heavy metal enzyme, and of oxygen in steady-state photosynthesis. Whittingham (1956) ascribes the prolonged induction period after anaerobic incubation in the dark to the accumulation of fermentation products, as does FRANCK (vide RABINOWITCH, monograph). During incubation in the dark with carbon monoxide, fermentation products will accumulate as well, so it may be expected that the effect on photosynthesis during the induction period is the same as with the anaerobic pretreatment. Therefore the assumption of any special effect of carbon monoxide on a reaction specific for photosynthesis is not justified.

Before discussing the experiments the technique used will be described. The arrangement consisted in the closed vessel described above (Fig. 1) and a water-cooled 500 watt projection lamp as a light source: VAN LOOKEREN CAMPAGNE (1957, Fig. 2). It is known that iron-carbonyl compounds are decomposed in light of the shorter wavelengths, but not in red light: WARBURG (1926, 1949). By comparing the influence of red and white light it is, therefore, possible to discriminate between iron-carbonyl and other carbonyl compounds. Red light was obtained by means of a Schott RG 5 glass filter transmitting only on the long wavelength side of 660 mμ. The light intensity could not be measured exactly because the Schott filter was frosted, but it was certainly not limiting the chloride absorption.

Carbon monoxide was generated by adding formic acid to hot sulfuric acid; it was purified by bubbling through alkali. The purified gas was stored over water. A gas mixture containing a small quantity of oxygen was prepared in the vessel in the following way: the vessel containing already the leaf strips was first filled with pure carbon monoxide, subsequently three quarters by volume of the gas was replaced by the chloride solution. The solution was saturated with air, consequently the resulting composition of the gas mixture after equilibration was calculated to be 1.7 % oxygen, 95 % carbon monoxide and the rest nitrogen. The calculation was not checked by analysis of the gases.

The first experiment was an indication that also in Vallisneria photosynthesis in red light is not inhibited by carbon monoxide. Oxygen was determined volumetrically. The gas phase was about 4.5 ml, therefore the error due to variations in atmospheric pressure and temperature was much larger than it was with the normal 2 ml gas phase. The light intensity was low: 5000 ergs cm^{-2} sec^{-1} red light. In the presence of carbon monoxide the oxygen production was 4.4. ± 0.4 μmoles per hour; without carbon monoxide 4.3 ± 0.3 μmoles per hour. Oxygen consumption in the dark, by the way, was not measurably inhibited by carbon monoxide, but perhaps the volume decrease recorded was not caused by the disappearance of oxygen only but partly by the disappearance of carbon monoxide, this gas possibly being hydrated to formic acid or oxidised to carbon dioxide.

When it was thus demonstrated that photosynthesis was unaffected it was tried whether carbon monoxide had any effect on chloride absorption. From Fig. 12 it is clear that carbon monoxide indeed inhibited chloride absorption in red light, but the inhibition was by no means total. In the dark chloride absorption was totally inhibited

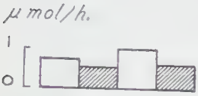
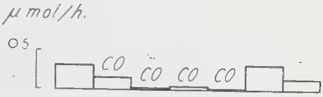


Fig. 12. Inhibition of chloride absorption by carbon monoxide in red light. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C; gas phase either air or 95 % CO +1.7 % O_2 + 3.3 % N_2.

(Fig. 13), in complete agreement with the data in literature (see above). The small absorption during the first period with carbon monoxide is probably not significant. Presumably some absorption occurred during the first few minutes after the vessel was filled, as this had to be done in the light.

Fig. 13. Influence of carbon monoxide on chloride absorption in the dark. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; gas phase either air or 95 % CO + 1.7 % O_2 + 3.3 % N_2.



The possibility existed that also in the light part of the chloride absorption is respiration-dependent, as it is in the dark, and that in the light only this respiration-dependent part of the chloride absorption was inhibited. Therefore, in a number of experiments the rate of uninhibited chloride absorption in the dark was compared to the degree of inhibition by carbon monoxide in red light. Examples are shown in Fig. 14. In some experiments the quantitative agreement was remarkable (A), but in other experiments the decrease in absorption in red light was significantly larger than the unhibited absorption in the dark (B). This can be explained in two ways: either the light-induced chloride absorption is slightly sensitive to carbon monoxide, or the respiration-dependent absorption is more or less

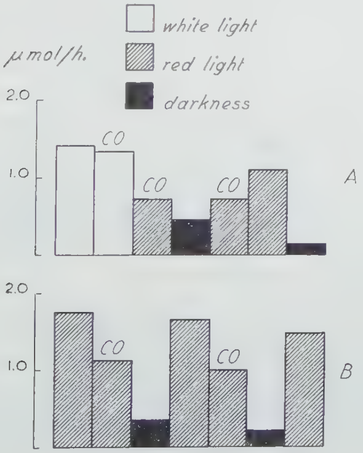


Fig. 14. Carbon monoxide inhibition of chloride absorption. Light-reversibility, and comparison with absorption in the dark. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; saturating red light; gas phase either air or 95 % CO + 1.7 % O_2 + 3.3 % N_2. A and B are separate experiments.

enhanced in the light, possibly by transference of intermediates of photosynthetic carbon dioxide assimilation or of reduced substances like DPNH from the sites of photosynthesis (chloroplasts) to the sites of respiration (mitochondria). The second explanation is considered the more likely one, because a sensitivity of the light-induced absorption process to carbon monoxide does not agree very well with the insensitivity of photosynthesis.

The substance or substances combining with carbon monoxide contain iron, as the inhibition present in red light is reversed by white light (Fig. 14A). The light-reversibility of the inhibition of absorption in the dark cannot, of course, be proved with certainty: any light causes light-dependent chloride absorption which obscures the expected reversion of the inhibition of the respiration-dependent absorption.

CHAPTER 7

ANAEROBIC CHLORIDE ABSORPTION

As the carbon monoxide experiments suggested that the light-dependent part of chloride absorption does not require the presence of free oxygen the influence of very low partial pressures of oxygen on chloride absorption was studied. The contents of the vessels were rendered and kept oxygen-free by aeration with pure nitrogen. The vessels were covered with a lid in order to keep air out. The nitrogen used for aeration had no measurable oxygen content, as was checked with reduced methylene blue; even when nitrogen was bubbled through for hours no blue colour reappeared.

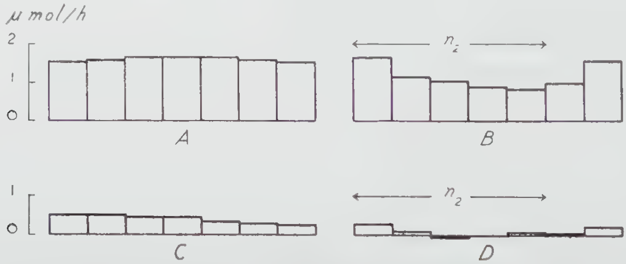


Fig. 15. Chloride absorption in the absence of oxygen in the light and in the dark. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; 7,000 ergs cm^{-2} sec^{-1} sodium light. Aeration with either air or pure nitrogen. A. Light; air, B. Light, nitrogen during the first five absorption periods. C. Dark, air; D. Dark, nitrogen during the first five absorption periods.

The experiments indicate a partial inhibition in the light and a total inhibition in the dark (Fig. 15). As with the carbon monoxide experiments the magnitude of the inhibition in the light is such that it is conceivable that only a respiration-dependent part of the absorption is inhibited, whereas the light-dependent absorption remains unaffected. In some experiments the inhibition gradually becomes much larger in the course of the experiment, which is probably caused by a gradual inactivation of an enzyme system somehow involved in the absorption mechanism.

The inhibition starts about one hour after the removal of oxygen and disappears also about one hour after oxygen is admitted again. Although highly improbable, the possibility exists that the removal of oxygen did not take less than one hour. It is, however, impossible that the penetration of oxygen through the tissue, when oxygen is admitted again, took more than a few minutes (cf. Fig. 3). It would seem probable, therefore, that the oxygen deficiency primarily results in the inactivation of the respiratory enzyme system only. This would be in agreement with the results of the carbon monoxide experiments.

The absence of a complete inhibition of chloride absorption does not, however, prove with certainty that free oxygen is not required in the absorption process. For notwithstanding all precautions to keep the partial pressure of oxygen as low as possible complete removal of all traces of oxygen could not be achieved, because Vallisneria leaves produce some oxygen in photosynthesis from the carbon dioxide liberated in fermentation. Diffusion through the tissue is not rapid enough to carry this oxygen and carbon dioxide away with sufficient efficiency.

CHAPTER 8

INHIBITION WITH CYANIDE

The other inhibitor yielding results worth mentioning was cyanide (strictly speaking hydrocyanic acid, HCN). Its action on chloride absorption is instantaneous and immediately and totally reversed upon removal of the inhibitor (Fig. 16). For these experiments the open vessels with aeration (Fig. 4) were used. The hydrocyanic acid stock solution was always freshly prepared from potassium cyanide and brought to pH 7 with sulfuric acid. The vessels were loosely covered with a lid in order to prevent evaporation of HCN. The quantity of HCN carried away with the aeration air stream was relatively small, as will be evident from the following calculation: The total air volume passing through the solution in a one-hour period is 200 ml, or less; the volume of the solution is 25 ml, so the air-to-liquid ratio is 200/25 = 8, or less. The partition coefficient of

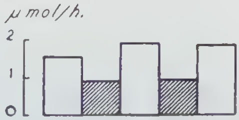


Fig. 16. Influence of 10^{-4} M hydrocyanic acid on chloride absorption. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; 7,000 ergs cm^{-2} sec^{-1} sodium light.

HCN between air and water at 18° C. is about 0.005 (molar units) at low HCN concentrations as calculated from data from the International Critical Tables vol. III p. 365; it was estimated to be not more than 0.01 at 24° C. It follows that at most $8 \times 0.01 = 0.08$, or 8 % of the HCN originally present could be carried away with the aeration stream in the course of one hour, which results in a mean HCN concentration not more than 4 % lower than the original concentration.

Following the incubation with Vallisneria leaf strips the 25 ml portions of experimental solution were evaporated to dryness in order to remove cyanide completely; the residues were dissolved again in water and chloride was titrated with silver nitrate in the normal way. Traces of cyanide would, of course, disturb the chloride determination. The respiration-dependent absorption is already totally inhibited at a cyanide concentration (10^{-4} M) at which the light-dependent absorption is only partly inhibited. The inhibition of the respiration-dependent absorption is presumably caused by the inactivation of cytochrome oxidase, as in the carbon monoxide experiments.

The rate of chloride absorption at light saturation is lowered, but at low light intensities the light-dependent part of chloride absorption is not inhibited (Fig. 17). The same was found with photosynthesis, as described below. The cyanide-sensitive substance, which limits chloride absorption in the light, must be insensitive or nearly insensitive to carbon monoxide and is, therefore, presumably not an autoxidisable heavy-metal compound. It is not possible to say whether or not it is involved in the chloride absorption process proper, although the experiments indicate (Fig. 18) that the cyanide inhibition becomes less pronounced with decreasing chloride concentration.

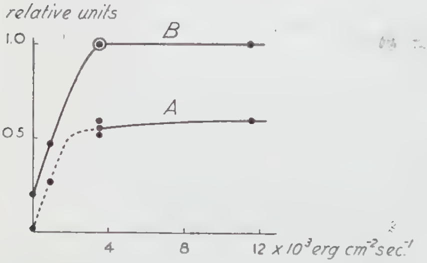


Fig. 17. Influence of light intensity on chloride absorption in the presence of hydrocyanic acid. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; sodium light. A. 10^{-4} M HCN; B. without HCN. Curve A is partly based on evidence from comparable experiments.

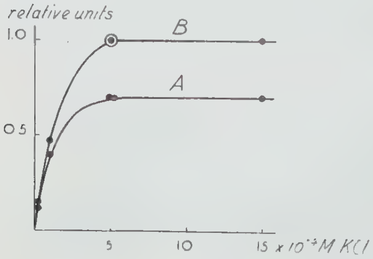


Fig. 18. Influence of chloride concentration on chloride absorption in the presence of hydrocyanic acid. Chloride solution with 2.5×10^{-4} M $CaSO_4$; 24° C.; 4500 ergs cm^{-2} sec^{-1} sodium light. A. 10^{-4} M HCN; B. without HCN.

The cyanide inhibition of chloride absorption is subject to long-term variations, as is also the case with the light intensity at which light saturation is reached (p. 553). The experiment shown in Fig. 19 was carried out three months later than the experiments described above: in the earlier experiments 10^{-4} M cyanide never caused more than 50 % inhibition in the light, but in this experiment the same concentration caused a nearly total inhibition. This result cannot be ascribed to experimental errors as the cyanide solution was always freshly prepared from the same stock of potassium cyanide. In photosynthesis such phenomena were not encountered.

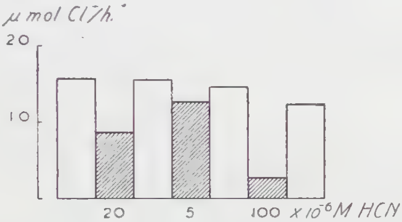


Fig. 19. Influence of hydrocyanic acid concentration on chloride absorption. 5×10^{-4} M KCl + 2.5×10^{-4} M $CaSO_4$; 24° C.; 7,000 ergs cm^{-2} sec^{-1} sodium light.

Photosynthesis in Vallisneria is also inhibited, which was to be expected according to literature. The literature of the inhibition of photosynthesis by cyanide is treated in detail by Rabinowitch in his monograph, to which may be referred here.

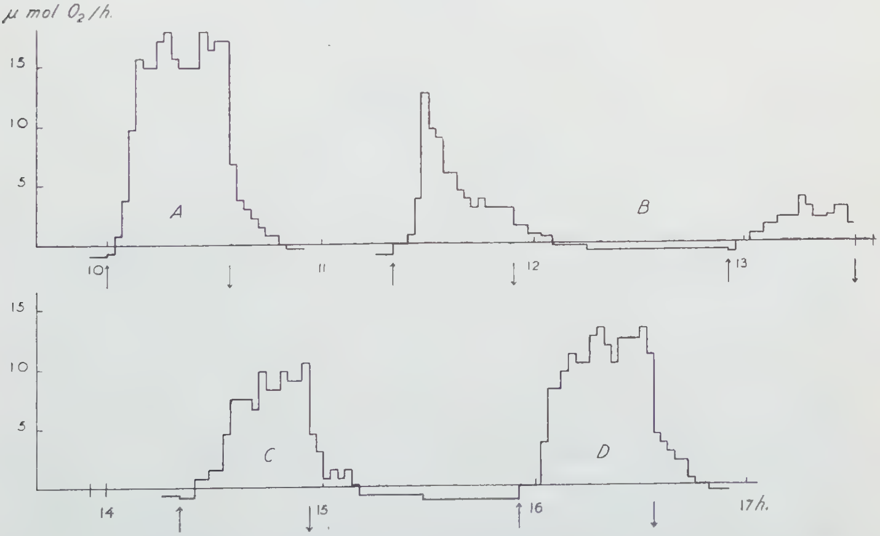


Fig. 20. Photosynthesis before adding hydrocyanic acid (A); in the presence of 3×10^{-5} M HCN (B); recovery after removal of HCN (C and D). 10^{-3} M CO_2 + 10^{-3} M $KHCO_3$ + 5×10^{-5} M $CaSO_4$, pH ∾ 6.4; 24° C.; 16,000 ergs cm^{-2} sec^{-1} sodium light (↑ light on; ↓ light off).

The experiments on the inhibition of photosynthesis by cyanide were carried out by means of the volumetric oxygen determination technique. They showed that the inhibition is not instantaneously maximal but increases gradually to its ultimate level (adaptation) (Fig. 20). The reversion of the inhibition (de-adaptation) is also gradual and it takes several hours before it is completed.

Surprisingly enough the adaptation reaction proceeds in the light only: even after prolonged incubation with cyanide in the dark photosynthesis starts with the peak shown in Fig. 20. Adaptation, once present, is not reversed again in the dark (Fig. 20B). Carbon dioxide reduction has no influence on the adaptation reaction, for, when illuminated in the absence of carbon dioxide Vallisneria leaves get adapted to cyanide at the same velocity as in the presence of carbon dioxide (Fig. 21).

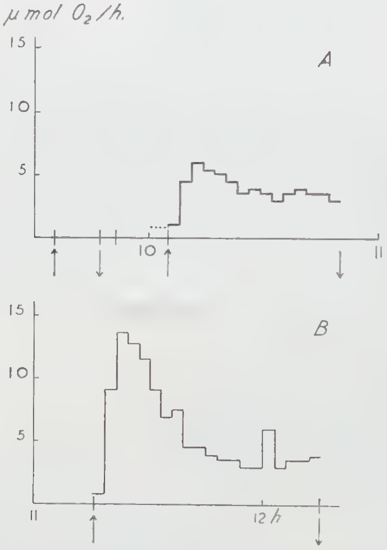


Fig. 21. Influence of carbon dioxide on the "adaptation" of photosynthesis to hydrocyanic acid. A. 12 minutes' pretreatment with 3×10^{-5} M HCN in the light in the absence of carbon dioxide; B. No pretreatment. Photosynthesis in a medium containing 10^{-3} M CO_2 + 10^{-3} M $KHCO_3$ + 5×10^{-5} M $CaSO_4$ + 3×10^{-5} M HCN, pH ∾ 6.4; 24° C.; 16,000 ergs cm^{-2} sec^{-1} sodium light (↑ light on; ↓ light off).

The substance reacting with cyanide is, therefore, probably not a constituent of the enzyme systems of carbon dioxide assimilation proper, nor of the liberation of oxygen from the primary oxidised product of water photolysis, because in both cases an influence of the presence of carbon dioxide on the adaptation reaction was to be expected; in the former case through carbon dioxide assimilation itself, in the latter case through the concomitant oxygen production.

At low light intensities photosynthesis after adaptation is not inhibited by cyanide (Fig. 22), so cyanide does not inhibit the process in which light energy is transformed into the first stable form of chemical energy. The remaining possibility is that cyanide primarily inhibits photosynthetic phosphorylation. This possibility will be treated more fully in the Discussion (Chapter 10).

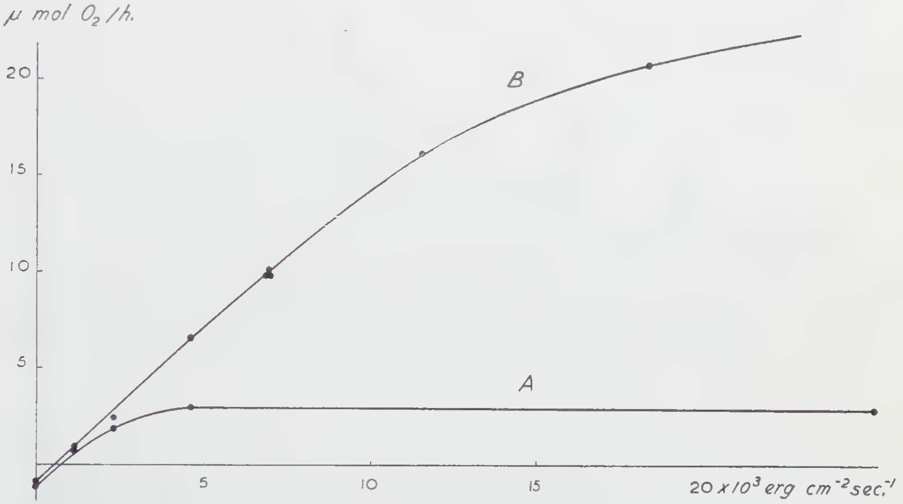


Fig. 22. Influence of light intensity on photosynthesis: A. in Vallisneria leaves fully adapted to hydrocyanic acid, B. in untreated leaves. 10^{-3} M CO_2 + 10^{-3} M $KHCO_3$ + 5 × 10^{-5} M $CaSO_4$, and either no inhibitor (B), or 3 × 10^{-5} M HCN (A); 24° C.; sodium light.

CHAPTER 9

PHOTOSYNTHETIC ASSIMILATION OF BICARBONATE

In Chapter 5 an experiment was described in which the influence of chloride on photosynthetic bicarbonate assimilation was examined. In view of the fact that in a previous paper I stated that Vallisneria leaves cannot utilise bicarbonate some explanation is needed here.

First it will be shown that oxygen is produced in a bicarbonate solution by Vallisneria leaves, which indicates that bicarbonate is utilised in photosynthesis. In this experiment the volumetric technique described on page 545-9 was used. The light intensity was 16.000 ergs cm^{-2} sec^{-1} sodium light. As a medium a 10^{-2} M potassium bicarbonate solution was given. Its pH was brought to 9.5 by adding potassium hydroxide. This was done in order to keep the carbon dioxide concentration too low to cause a measurable oxygen production: the carbon dioxide concentration was less than 10^{-5} M.

As shown in Fig. 23 the oxygen production was quite large, but it took about one hour to attain the steady-state. The rate of oxygen production finally attained was about one half the maximum rate possible in carbon dioxide assimilation. It was found earlier that in the absence of carbon dioxide and bicarbonate there is no photosynthetic oxygen production in Vallisneria: VAN LOOKEREN CAMPAGNE (1955).

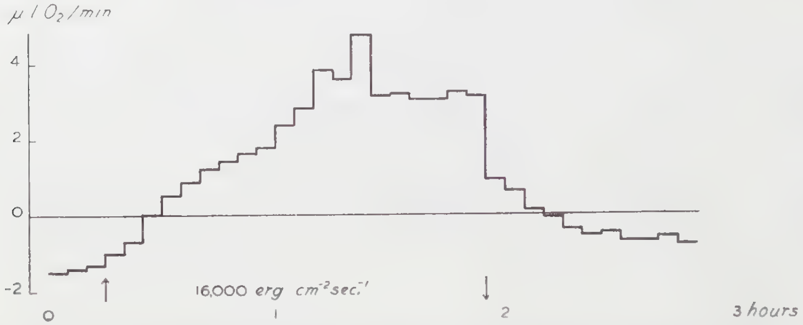


Fig . 23. Photosynthetic oxygen production in Vallisneria leaves from 10^{-2} M $KHCO_3$ + 5 × 10^{-5} M $CaSO_4$. Initial pH 9.5; final pH 9.7; 24° C.; 16,000 ergs cm^{-2} sec^{-1} sodium light (↑ light on; ↓ light off).

When the time course of oxygen production from bicarbonate and from carbon dioxide (Fig. 24) are compared a striking difference will be noticed. With carbon dioxide the oxygen production suddenly starts at full speed after some three minutes' time lag. This time lag cannot be explained by slow response of the volumeter to changes in the oxygen production rate, because the volume change per minute recorded is proportional to the oxygen concentration difference between the leaf tissue and the gas bubble in the vessel, and will, therefore, begin at about the same moment the oxygen production begins. If the oxygen production started immediately upon illumination

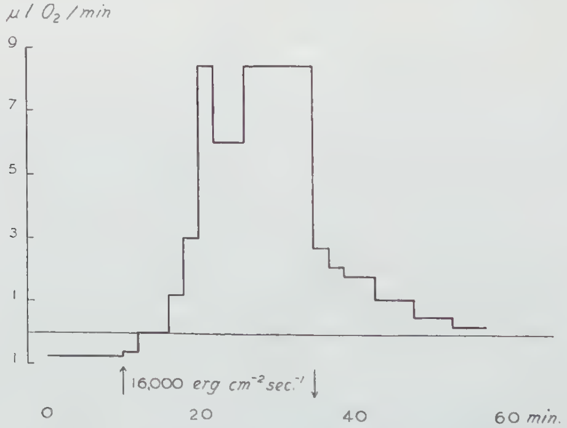


Fig. 24. Photosynthetic oxygen production in Vallisneria leaves from carbon dioxide. 10^{-3} M CO_2 + 10^{-3} M $KHCO_3$ + 5 × 10^{-5} M $CaSO_4$, pH ∾ 6.4; 24° C.; 16,000 ergs cm^{-2} sec^{-1} sodium light.

at full rate the volume changes recorded would increase exponentially until the maximum rate is approached. An S-shaped curve like the one in Fig. 24, therefore, indicates a real lag in the oxygen production.[1]) The duration of the lag period does not depend perceptibly on light intensity. (The apparent oxygen production after the light is turned off can be ascribed to the rather slow gas exchange between the intercellular gas spaces in the leaf strips and the surrounding medium (cf. Fig. 3).) With bicarbonate the oxygen production gradually increases for a considerable length of time (Fig. 23), before attaining the steady-state with some unexplained fluctuations. It seems, therefore, as if a considerable length of time is required before the leaves are adapted to the utilisation of bicarbonate, a phenomenon encountered in *Scenedesmus* by ÖSTERLIND (1951). Possibly, however, the very high pH was an interfering factor with Vallisneria, which is suggested by the fact that the oxygen consumption in the dark is always strongly enhanced in such alkaline media: it often amounts to some five times the normal respiration rate which is about 0.6 μmoles oxygen per hour.

The oxygen production from a certain bicarbonate concentration is quite variable, much more than is the case with carbon dioxide. The optimum lies in the range of 10^{-2} M bicarbonate.

For the explication of the divergent conclusion of the earlier experiments: VAN LOOKEREN CAMPAGNE (1955), it is important to realise how they were carried out. Experimental periods with only carbon dioxide in a low concentration alternated with periods in which 10^{-3} M potassium bicarbonate was given in addition. The oxygen production found was the same whether bicarbonate was present or not, a result repeatedly obtained. The crucial point is that the experimental periods during which the leaf strips were in the light were 20 minutes and that during the periods between, also about 20 minutes, the leaf strips were in the dark. The apparent absence of bicarbonate utilisation, then, can be explained when it is realised that owing to the short light period and the low bicarbonate concentration the bicarbonate utilisation had not the opportunity to attain a measurable rate.

It must be admitted that it was to be expected that Vallisneria leaves would be capable of utilising bicarbonate, because all submersed phanerogams investigated thus far can do it: ARENS (1933, 1936), RUTTNER (1947, 1948), STEEMANN NIELSEN (1947, 1951, 1952). Ruttner, indeed, concluded from his experiments that also Vallisneria can utilise bicarbonate in photosynthesis (1947), a conclusion no longer at variance with the results of this investigation.

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[1]) The apparent lag might also be explained if the photosynthetic quotient largely exceeds minus unity during the first few minutes in the light.

CHAPTER 10

DISCUSSION

The subject of this paper is a phenomenon somewhat arbitrarily called chloride absorption. The mere reason for this is that the absorption of the chloride ions only was measured, and not that of cations. It is by no means certain that the anion especially is actively absorbed, and that the cation is passively carried along. The reverse is equally possible. More plausible in the author's opinion is that in any part of the absorption process both anion and cation, perhaps together, are transported by means of a mechanism utilising some kind of metabolic energy.

The results of the investigation described here indicate that the active chloride absorption in Vallisneria leaves consists of two parts differing in their source of energy. One part is a conventional respiration-dependent chloride absorption which proceeds in the dark as well as in the light, and which is inhibited by carbon monoxide, cyanide, and oxygen deficiency. From the carbon monoxide inhibition it was concluded that cytochrome oxidase is directly or indirectly involved in this part of the process. As cytochrome oxidase is localised in particles, presumably mitochondria only: Millerd (1956), the activities of these particles must be taken into consideration when this respiration-dependent part of chloride absorption is discussed. Chloroplasts probably do not contain significant amounts of cytochrome oxidase: McClendon (1953).

The other part of the chloride absorption is light-dependent, and is not inhibited by carbon monoxide. In this process chlorophyll is involved, so in the case of light-dependent chloride absorption the activities of the chloroplasts must be taken into consideration.

The question arises as to how, and where, light energy and respiratory energy respectively are utilised in the absorption process proper. First there is the possibility that the energy-consuming part of the absorption process occurs in the mitochondria as far as it is respiration-dependent, cf. Robertson (1951), and in the chloroplasts for the part which is light-dependent. This gives rise to the problem as to how the ions reach these particles across the cell membrane, and how they are transferred from mitochondria and chloroplasts to the vacuoles without being dissipated again. This problem could be circumvented by the assumption that there is no impermeable cell membrane, and that the transfer takes place by means of an ion-carrier complex. It is fairly certain that the chloride ions absorbed are, at least partly, transferred into the vacuoles, because chloride absorption causes an increase in the osmotic value of the vacuole contents, as was demonstrated by Miss A. van Schreven and by Miss. A. G. van der Molen: Arisz (1943, 1956). All this makes it improbable that all chloride absorbed should remain accumulated in the mitochondria and chloroplasts.

The second possibility is that mitochondria and chloroplasts merely serve as generators of energy, the energy being utilised elsewhere in the cell in the energy-consuming reactions of ion absorption. This necessitates the assumption that the energy supply is the limiting factor in absorption as long as the absorption rate is below its maximum level, because otherwise the respiration-dependent and the light-dependent chloride absorption could not be quantitatively separated as was done in the carbon monoxide experiments.

Which of those two possibilities may be realised: whether the ions are fixed onto carriers at mitochondria and chloroplasts, or for instance at the outer cytoplasmic layers or at the tonoplast, in either case it is attractive to assume that the absorption process or processes derive their energy in one and the same chemical form both from respiratory and from light energy. To the extent this is in the form of an oxidation-reduction reaction sequence it would imply one of the three following possibilities: 1. Chloride is accumulated in chloroplasts and mitochondria before transfer into the vacuole is possible. This is improbable as discussed above. 2. Chloride is fixed to a carrier at chloroplasts and mitochondria, and released into the vacuole at the tonoplast. a. A carrier is reduced at chloroplasts and mitochondria in the act of ion fixation, and molecular oxygen is necessary in order to oxidise the ion-carrier compound again in ion liberation. This is, at least in the case of light-dependent chloride absorption unlikely in view of the experiments on the effect of oxygen deficiency and carbon monoxide, which rendered it probable that molecular oxygen is not required. b. Two substances are generated in chloroplasts and mitochondria, a reduced one and an oxidised one, one of them an ion-carrier complex. The two substances are then brought into reaction with each other at the tonoplast, thereby releasing the ion(s) from the complex. This possibility is related to the third. 3. The absorption process is localised entirely outside mitochondria and chloroplasts. Here again two substances should be generated, a reduced one and an oxidised one, one or perhaps both of them acting as carriers of cation and anion respectively. These two possibilities are not improbable. The production of reducing power, it is true, cannot be inhibited by carbon monoxide or anaerobiosis, because it is generated in fermentation if respiration is prevented, and because photosynthesis is not inhibited by carbon monoxide or anaerobiosis. The production of oxidising power in mitochondria, however, could conceivably be inhibited by carbon monoxide and anaerobiosis, thereby explaining the inhibition of respiration-dependent absorption alone. There remain, therefore, the possibilities 2b and 3, if an oxidation-reduction reaction sequence is involved in chloride absorption.

The effects of cyanide, however, and the induction lag phenomena (see below) suggest another possibility, *viz.* that energy-rich phosphates (e.g. adenosine triphosphate: ATP) supply the energy required. In this case the inhibition of the respiration-dependent absorption by carbon monoxide and anaerobiosis is readily explained, as phosphorylation in mitochondria is largely dependent on the proper functioning of the cytochrome system and this is inactivated by carbon monoxide and anaerobiosis. The light-dependent absorption would then utilise energy-rich phosphates generated in "photosynthetic phosphorylation": ARNON (1956) in the chloroplasts. Photosynthetic phosphorylation proceeds optimally in the absence of oxygen, so Arnon supposes that the energy required is derived from the recombination of the products of water photolysis; see also WESSELS (1957). As free oxygen is not involved in this reaction it is conceivable that carbon monoxide has no influence on photosynthetic phosphorylation, and consequently on neither photosynthesis nor light-dependent chloride absorption. It is also in agreement with the finding that at low oxygen tension the light-dependent absorption proceeds unimpaired (Fig. 15).

As said in Chapter 8 the inhibition of photosynthesis by cyanide is probably not caused by the blocking of the mechanism which transforms light energy into the first stable form of chemical energy, nor that involved in carbon assimilation, nor that which brings about the conversion of the primary oxidised product of water photolysis into free oxygen. The only remaining possibility is that cyanide primarily inhibits photosynthetic phosphorylation in Vallisneria leaves. According to ARNON *et al.* photosynthetic phosphorylation in chloroplast suspensions is indeed inhibited by cyanide (1956). If it is true that energy-rich phosphates are the source of energy in chloride absorption in Vallisneria leaves, the possibility obviously exists that photosynthesis and light-dependent chloride absorption have some partial process reaction in common which is inhibited by cyanide. Experimental evidence is, however, insufficient to substantiate this hypothesis. Also the objection could be raised against it that the inhibition of chloride absorption by cyanide is rapidly reversed, whereas the capacity for photosynthesis is rather slowly restored. This difficulty could be avoided if one assumes that a low degree of inhibition of the common reaction does not yet lead to inhibition of the chloride absorption. This assumption is by no means unreasonable in view of the fact that chloride absorption is light-saturated at a light intensity much lower than required for photosynthesis (Fig. 7). For if photosynthesis proceeds at a rate of e.g. 5 μmoles oxygen per hour at the light intensity at which chloride absorption is just saturated, it is quite possible that (at higher light intensities) chloride absorption is no longer inhibited as soon as photosynthesis proceeds at a rate higher than 5 μmoles oxygen per hour. Such a partial reversion of cyanide inhibition presumably takes no more than some ten minutes.

In connection with the problem of the sites where energy is utilised in the absorption process the following remark on the question of the permeability of the outer cytoplasmic layer might be made. It has been suggested that the cytoplasm is, at least partially, freely accessible to ions, because in free-space experiments ions and uncharged molecules were found to penetrate into a space that could not be accounted for by cell walls and interstices only (for references vide EPSTEIN (1956).) This is often thought to indicate that the outer cytoplasmic layer is permeable to all small molecules and ions. A free accessibility of the cytoplasm would imply that the internal ion concentrations, and consequently the pH would be directly dependent on the external ion concentrations and pH. But as many organisms like Vallisneria are not impaired in their activities even at a quite high pH in the medium (up to pH 10, or more), and other organisms can tolerate a very low pH, free accessibility of the cytoplasm to all ions, among which hydrogen and hydroxyl ions, would mean that the proteins (enzymes) of these organisms remain stable, and active, at quite extreme pH values. This, now, seems rather improbable, which constitutes an argument in favour of the theory that the cytoplasm has an outer layer which is relatively impermeable to ions; see also WALKER (1957).

The results of the free-space experiments mentioned above might be explained by assuming that the ion combines reversibly with a specific carrier, and that the ion-carrier complex is capable of crossing the membrane the free ion is not. If such a carrier exists for certain substances only and not for e.g. hydrogen and hydroxyl ions there is no incompatibility between the free accessibility found in the free-space experiments and the toleration of extreme pH values. Therefore, an outer cytoplasmic layer which is impermeable to free ions is not necessarily in contradiction with the results of the free-space experiments. On the ground of these considerations among other ones I should like to suppose that any ion to be absorbed or exchanged has to cross an outer cytoplasmic layer as an ion-carrier compound: cf. ARISZ (1954 II).

Now, with Vallisneria chloride ions are not given off to the medium when the leaves are healthy, so in this case there may be some advantage in supposing a somewhat different mechanism for the passage of chloride ions from the medium into the cytoplasm, *viz.* a mechanism as proposed by MITCHELL (1957). The essential feature of this mechanism is that an ion-carrier compound, once formed, cannot dissociate again, but that another ion of the same or a related species can replace the ion combined with the carrier, or that the combined ion can be transferred to another substance, or liberated in a process for which metabolic energy is required. In this case no net absorption or secretion (leakage) can occur if there is no energy available, but exchange remains always possible.

This mechanism offers the possibility that ions, after being bound to a membrane-bound carrier, are transferred to another substance with carrier function which can freely move about through the cytoplasm, and from cell to cell through the symplasm (parenchymatic long-distance transport): ARISZ and OUDMAN (1937), ARISZ and SCHREUDER (1956 I), ARISZ (1954 I, 1956). The ion then could be translocated without ever getting free in the cytoplasm and merging into a pool of free ions eventually present in the cytoplasm. At the tonoplast a comparable carrier mechanism could transfer the ions from the "cytoplasmatic carrier" across the tonoplast and liberate them into the vacuole.

The hypothesis could be very helpful in explaining how in photosynthetic bicarbonate assimilation bicarbonate ions could be transferred from the medium to the chloroplasts without rapidly dissociating into hydroxyl ions and carbon dioxide, which would be the case if the ions occurred in free state in the cytoplasm. If they did dissociate, the resulting carbon dioxide molecules could not be prevented from diffusing out again, and there would be no possibility that bicarbonate could enhance photosynthesis. But if, according to the hypothesis outlined above, the bicarbonate ions travel through the cytoplasm as an ion-carrier compound in which the bicarbonate ions are stabilised, dissociation into carbon dioxide and hydroxyl ion is prevented, and bicarbonate can be assimilated at a high rate even at very low carbon dioxide concentration. There is good reason to suppose that chloride ions and bicarbonate ions are translocated by means of separate mechanisms, for it was found that chloride absorption is inhibited by bicarbonate, whereas bicarbonate assimilation is not inhibited by chloride (Chapter 5). Apparently the chloride-specific mechanism can be blocked by bicarbonate ions; the bicarbonate-specific mechanism, which may be a carboxylating mechanism, is insensitive to chloride ions.

Next some comment should be given on the connection between the experiments reported in this paper and the investigations of Arisz *et al.* on chloride absorption in Vallisneria during 24 hours' periods. Arisz (1953, 1956) found that cyanide inhibits specifically the uptake of chloride from the medium into the symplasm of Vallisneria leaves, but not the transfer from the symplasm into the vacuoles or the transport along the leaves.

Arisz explains these facts by assuming that cyanide inhibits a process in which chloride is transferred through the outer layers of the cytoplasm. In terms of Mitchell's theory this might be interpreted as an inhibition by cyanide of the transfer of the ions by a carrier, possibly by cutting off the supply of the energy required in the process, which might mean that it is not a carbohydrate derivative.

From their experiments on the influence of pre-illumination Arisz and Sol (1956) conclude that in the light a substance is formed in Vallisneria leaves which promotes chloride absorption. This substance is probably another than is involved in the effect of sucrose. The substance is transportable, as was shown in experiments in which the leaf strips were only partly immersed in the chloride solution. When the "free" parts (immersed in distilled water) were in the light the "absorbing" parts (immersed in chloride solution) absorbed more chloride than when the free parts were in the dark. Arisz and Sol tentatively ascribe a carrier function to the substance. The present author would suggest the identity of the substance with a carrier to which the ions are fixed, and in combination with which they travel about through the symplasm.

In the present investigation no indication was obtained that a substance was formed in the light. This result was certainly due to the short duration of the experiments and their design which differed greatly from the way the experiments by Arisz and Sol were carried out.

The enhancing effect of sucrose on chloride absorption: ARISZ and SOL (1956) might be ascribed to a stimulation of the respiration-dependent production of energy-rich phosphate. This then causes an increased respiration-dependent absorption of chloride and possibly also promotes the transport of an ion-carrier complex.

With 2,4-dinitrophenol ARISZ (1953) could inhibit specifically the passage of chloride into the vacuole, whereas the uptake from the medium and the transport along the leaf strips was less impaired.

Other inhibitors as azide yielded comparable results, which were, however, better reproducible (ARISZ, unpublished results). The results with dinitrophenol might be interpreted as an indication that energy-rich phosphates are needed for the secretion of the ions into the vacuoles, but not for the preceding uptake into the symplasm or the fixation to a carrier, as the case may be. The present author, however, found in short-duration experiments that the inhibition of chloride absorption caused by dinitrophenol begins slowly, increases slowly in the course of hours and continues to increase even when the inhibitor is no longer present in the medium. In his opinion, therefore, the inhibition by dinitrophenol seems to be indirect and not necessarily an indication that energy-rich phosphates are required in the part of the process which is inhibited by dinitrophenol. The inhibition by azide likewise was neither constant nor completely reversible.

A phenomenon remaining to be discussed is the induction lag shown in photosynthesis (Fig. 24). It might be supposed that photosynthetic phosphorylation does not start immediately after the light is turned on, thereby delaying the onset of carbon assimilation. The supposition is based on the fact that the adaptation reaction to cyanide (Chapter 8, p. 563) proceeds in the light only.

If, as made likely above, cyanide primarily inhibits photosynthetic phosphorylation, it follows that the enzyme system involved in this reaction changes its reactivity to cyanide upon illumination. This change in reactivity to cyanide indicates a chemical transformation which then is supposed to bring about the activation of the enzyme system. It is not too far-fetched to suppose that this chemical transformation will take some minutes' time, thereby delaying the onset of photosynthetic phosphorylation for a same period of time.

This possibility to explain induction effects was not yet considered by RABINOWITCH in his monograph (II^2 1956). In the author's opinion it is not at a variance with data from the literature on induction effects. WASSINK and KATZ (1939) for instance found with Chorella that in cyanide-poisoned cells fluorescence does not decrease again after a maximum rate is reached within the first minute in the light, as it does in uninhibited cells. If one assumes that strong fluorescence can be caused by the inactivity of the enzyme system of photosynthetic phosphorylation: cf. STREHLER (1952), and that cyanide inhibits photosynthetic phosphorylation in Chlorella as it is supposed to do in Vallisneria it is plausible to ascribe the induction lag period in Chlorella as well as in Vallisneria primarily to a temporary inactivity of the mechanism of photosynthetic phosphorylation, which then is prolonged *ad infinitum* after adaptation to cyanide.

Tentatively it is suggested that the chemical transformation (activation) of the enzyme system of photosynthetic phosphorylation might consist in an oxidation of a heavy-metal compound (cytochrome) because especially oxidised heavy-metal compounds react with cyanide. Alternatively an oxidation of an alcoholic group (e.g. in ascorbic acid) to a carbonyl compound might be suggested, the =CO-group also reacting reversibly with cyanide: James (1953 I, 1953 II).

Light-induced chloride absorption shows, when the light is turned on, a comparable time lag as photosynthesis in Vallisneria (Chapter 3, Fig. 6). This suggests that a common process is limiting during the induction phase. If one or more stages of the chloride absorption process require energy-rich phosphates as the source of energy this common process is presumably photosynthetic phosphorylation. If, on the other hand, chloride absorption is brought about by one or more oxidation-reduction reactions exclusively, it might be supposed that the generation of the reduced or of the oxidised substances or both requires energy-rich phosphates. (It has been suggested that the reduction of pyridine nucleotide in chloroplasts requires the energy of ATP; Strehler (1952). This is, however, not supported by recent results obtained by Arnon *et al.* (1957). It cannot, of course, be excluded that the induction lag in chloride absorption has nothing to do with the lag in photosynthesis.

The resulting picture of the chloride absorption process in Vallisneria leaves is the following: chloride ions and accompanying cations diffuse passively through the cell wall; subsequently the ions are bound to a carrier with the help of metabolic energy, presumably at the outer cytoplasmic boundary, in order to cross an outer layer which is impermeable to ions; perhaps the ions remain bound in the form of some kind of ion-carrier compound which is carried about from cell to cell in the symplasm; and finally at the tonoplasts the ions are somehow transferred into the vacuoles with or without the utilisation of metabolic energy. This picture possibly holds also for ion absorption in plant roots and other ion transport processes, but it is beyond the scope of this paper to extend the hypotheses thus far.

SUMMARY

The light-dependent chloride absorption in Vallisneria leaves was studied in its relation to the respiration-dependent chloride absorption, and to photosynthesis.

Light-dependent chloride absorption begins at full rate some five minutes after the light is turned on; it ends within two minutes after the light is turned off (Fig. 6). Light saturation is reached at a much lower light intensity than with photosynthesis (Fig. 7).

The action spectra of chloride absorption and photosynthesis are identical (Fig. 8), so chlorophyll is involved in light-dependent chloride absorption.

Carbon dioxide has no instantaneous influence on chloride absorption in the light, which proves the absence of a direct relationship between chloride absorption and carbon assimilation. Bicarbonate ions inhibit chloride absorption in the light

as well as in the dark, but chloride ions do not inhibit photosynthetic bicarbonate assimilation.

Carbon monoxide inhibits the respiration-dependent chloride absorption only; it has no influence on light-dependent chloride absorption or photosynthesis (Chapter 6). The same probably holds for oxygen withdrawal (Chapter 7).

Cyanide inhibits chloride absorption instantaneously and fully reversibly. The inhibition of photosynthesis increases gradually when the leaf tissue is in the light until a stationary level is reached; in the dark the reaction with cyanide which causes the inhibition does not take place at all (Fig. 20). The inhibition is gradually reversible.

In Chapter 9 the photosynthetic assimilation of carbon dioxide and bicarbonate has been treated; a correction of an earlier paper on photosynthesis in Vallisneria has been included there.

The experimental data are discussed in Chapter 10.

ACKNOWLEDGEMENTS

This investigation was carried out between 1954 and 1957 at the Botanical Laboratory, Groningen, aided by a grant from the Netherlands Organization for Pure Research (Z.W.O.). I wish to express my sincerest thanks to Prof. dr. W. H. Arisz, who suggested the problem and offered valuable advice and criticism. Prof. dr. M. Gruber kindly made valuable suggestions concerning the Appendix. To him and to all those who assisted during the investigation and in the preparation of the manuscript I am much indebted.

APPENDIX

DERIVATION OF THE VOLUMETER EQUATION

The volumeter is essentially a vessel partly filled with a watery solution in equilibrium with a gas phase which is kept at constant pressure and temperature. The water phase contains a certain amount of the gases in solution, in the case of air essentially nitrogen, oxygen and a little carbon dioxide. If, e.g. by photosynthesis, a small amount of oxygen is produced within the volumeter and a proportional amount of carbon dioxide is simultaneously removed, the vessel being shaken, a new equilibrium will be established. Part of the oxygen produced will pass into the gas phase and will therefore cause an increase in the oxygen partial pressure. Carbon dioxide is much more soluble than oxygen, therefore the carbon dioxide removed will for a relatively greater part be derived from dissolved carbon dioxide. Consequently the decrease in carbon dioxide in the gas phase and the concomitant decrease in its partial pressure will be smaller than the increase in oxygen in the gas phase and its partial pressure. As the total gas pressure is kept constant the increase in oxygen partial pressure (minus decrease in carbon dioxide partial pressure) will cause a decrease in the nitrogen partial pressure, and this in its turn will cause nitrogen to pass from the liquid to the gas phase. From this reasoning it will be clear that the gas exchanges occurring are quite complicated and that, especially when the liquid volume is large compared to the volume of the gas phase, the influence of changes in partial pressure and amount dissolved of any of the gases present, even nitrogen, cannot be neglected.

Therefore an equation was derived in the following way:

If V_G = initial volume of the gas phase

V'_G = final volume of the gas phase

V_L = initial volume of the liquid phase

V'_L = final volume of the liquid phase ($V'_L = V_L$)

$\triangle V$ = increase in volume ($\triangle V = V'_G - V_G$)

p_{O_2}; p_{CO_2}; p_{N_2}; p_{CO}; p_{H_2O} = initial partial pressures of the gases

p'_{O_2}; p'_{CO_2}; p'_{N_2}; p'_{CO}; p'_{H_2O} = final partial pressures

$\triangle p_{O_2}$; $\triangle p_{CO_2}$; $\triangle p_{N_2}$; $\triangle p_{CO}$ ($\triangle p_{H_2O} = 0$) = changes in partial pressure

p_S = total gas pressure minus water vapour pressure

s_{O_2}; s_{CO_2}; s_{N_2} s_{CO}; = solubility factors of the gases (expressed as volume units of gas at prevailing temperature which are dissolved in one volume unit of water in equilibrium with a gas phase consisting of the gas concerned only). The solubility factors are assumed to be independent of the composition of both gas- and liquid phases.

$\triangle O_2$ = increase in oxygen (volume units at prevailing temperature and atmospheric pressure minus water vapour pressure)

$\triangle CO_2$ = increase in carbon dioxide (same units) ($\triangle CO_2 = -Q \times \triangle O_2$, in which Q = photosynthetic quotient)

then:

1. Initial total quantity of oxygen = $(V_G + s_{O_2}V_L)p_{O_2}$ (energy units)

1a. Final total quantity of oxygen = $(V'_G + s_{O_2}V'_L)p'_{O_2}$ = $(V_G + \triangle V + s_{O_2}V_L)(p_{O_2} + \triangle p_{O_2})$

1b. but also = $(V_G + s_{O_2}V_L)p_{O_2} + \triangle O_2 p_S$

From equations 1a and 1b $\triangle p_{O_2}$ can be obtained explicitly:

2. $$\triangle p_{O_2} = \frac{-\triangle V p_{O_2} + \triangle O_2 p_S}{V_G + \triangle V + s_{O_2} V_L}$$

2a. In the same way $\triangle p_{CO_2}$ =

$$\frac{-\triangle V p_{CO_2} - \triangle CO_2 p_S}{V_G + \triangle V + s_{CO_2} V_L} = \frac{-\triangle V p_{CO_2} + Q \triangle O_2 p_S}{V_G + \triangle V + s_{CO_2} V_L}$$

2b. and $$\triangle p_{N_2} = \frac{-\triangle V p_{N_2}}{V_G + \triangle V + s_{N_2} V_L}.$$

The total gas pressure is kept constant; p_{H_2O} is constant, because the temperature is constant; therefore p_S is constant,

3. so $\Delta p_{O_2} + \Delta p_{CO_2} + \Delta p_{N_2} = 0$

In this equation Δp_{O_2}, Δp_{CO_2}, Δp_{N_2} can be eliminated by means of 2, 2a, 2b and then the equation can be solved for $\Delta O_2/\Delta V$:

$$4. \quad \frac{\Delta O_2}{\Delta V} = \frac{1}{p_s} \times \frac{(V_G+\Delta V)^2 p_s + (V_G+\Delta V) V_L \{(s_{CO_2}+s_{N_2})\, p_{O_2} + (s_{O_2}+s_{N_2})\, p_{CO_2} + (s_{O_2}+s_{CO_2})\, p_{N_2}\} + V_L^2 (s_{CO_2} s_{N_2} p_{O_2} + s_{O_2} s_{N_2} p_{CO_2} + s_{O_2} s_{CO_2} p_{N_2})}{(1+Q)(V_G+\Delta V)^2 + (V_G+\Delta V) V_L \{s_{CO_2} + Q s_{O_2} + (1+Q) s_{N_2}\} + V_L^2 (s_{CO_2} s_{N_2} + Q s_{O_2} s_{N_2})}$$

In this equation the value of $\Delta O_2/\Delta V$ is dependent on the value of ΔV. Theoretically, therefore, $\Delta O_2/\Delta V$ should be calculated for each single value of ΔV. Under certain experimental conditions, however, the influence of ΔV on $\Delta O_2/\Delta V$ can be neglected, as may be seen from the following calculation:

With the apparatus used here (Fig. 2) 0.2 ml is the maximal value ΔV can attain; the minimal value is, of course, zero. Consequently the largest possible change in $(V_G + \Delta V)$ is 0.2 ml. Now, in Fig. 25 curve 1 $\Delta O_2/\Delta V$ is plotted as a function of $(V_G + \Delta V)$, the gas phase assumed to consist of air with 2 % carbon dioxide and the liquid phase to be 15 ml. If under these conditions V_G is at least 0.9 ml it may be seen from Fig. 25 curve 1 that the change in $\Delta O_2/\Delta V$ corresponding to a 0.2 ml change in $(V_G + \Delta V)$ is not more than 0.01, or about 1 percent of the total value of $\Delta O_2/\Delta V$; 1 percent is well within the experimental error. In the experiments described here V_G was 1 ml or more, which makes the error in $\Delta O_2/\Delta V$ even

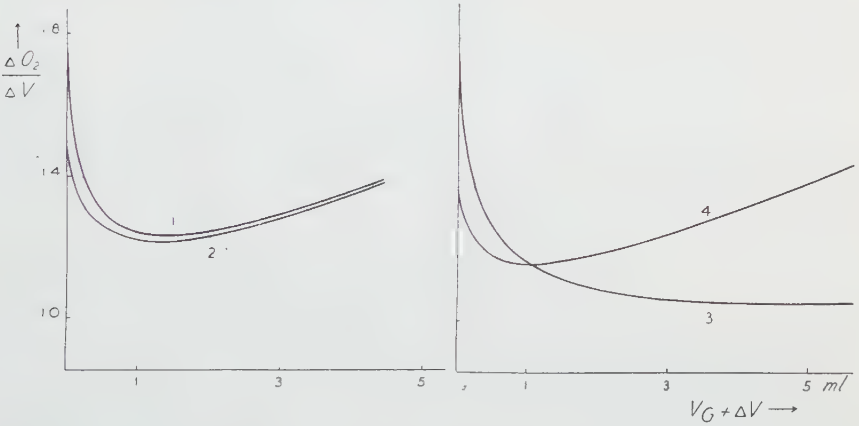

Fig. 25. Curves showing $\Delta O_2/\Delta V$ (oxygen produced in photosynthesis versus volume change recorded with the volumeter) plotted as a function of $(V_G + \Delta V)$ (final volume of the gas phase in the volumeter. Curve 1. gas phase 20 % O_2, 2 % CO_2, 78 % N_2; curve 2. gas phase 49 % O_2, 2 % CO_2, 49 % N_2; curve 3. gas phase 20 % O_2, 80 % N_2, liquid phase bicarbonate solution at pH 9 or more; curve 4. gas phase 1.7 % O_2, 2 % CO_2, 3.3 % N_2, 93 % CO. Liquid phase assumed to be 15 ml watery solution in all curves.

smaller. If, however, V_G is e.g. 0.3 ml the change in $\triangle O_2/\triangle V$ corresponding to a 0.2 ml change in $(V_G + \triangle V)$ is about 0.14, or more than 10 %.

A similar calculation was applied for the other experimental conditions occurring in the various experiments.

In practice apart from $\triangle V$ many of the terms in the numerator and denominator of the right-hand side of equation 4 can be neglected:

$$4a. \quad \frac{\triangle O_2}{\triangle V} = \frac{1}{p_s} \times \frac{V_G{}^2 p_s + V_G V_L (s_{CO_2} p_{O_2} - s_{CO_2} p_{N_2}) + V_L{}^2 s_{CO_2} s_{N_2} p_{O_2} + s_{O_2} s_{CO_2} p_{N_2})}{(1+Q) V_G{}^2 + V_G V_L s_{CO_2} + V_L{}^2 s_{CO_2} s_{N_2}}$$

If Q = —1 the term (1 + Q) V_G becomes zero (Fig. 25, curves 1, 2). In the experiments gas phase air with 2 % CO_2; $V_G = 2$ ml): $\triangle O_2/\triangle V = 1.20$.

With a bicarbonate solution at a pH higher than 9 there is no molecular carbon dioxide present in the vessel, therefore Q is virtually zero and all CO_2 parameters in equation 4 have to be omitted. The result is:

$$4b. \quad \frac{\triangle O_2}{\triangle V} = \frac{1}{p_s} \times \frac{V_G p_s + V_L (s_{N_2} p_{O_2} + s_{O_2} p_{N_2})}{V_G + V_L s_{N_2}} \quad \text{(Fig. 25, curve 3)}$$

In the experiments (gas phase air; $V_G = 1$ ml): $\triangle O_2/\triangle V = 1.13$

With a gas phase consisting mainly of carbon monoxide the terms containing p_{O_2} and p_{CO_2} as factors can be neglected; all nitrogen parameters in the equation are replaced by the corresponding carbon monoxide parameters; $p_s = p_{CO}$.

The resulting equation is:

$$4c. \quad \frac{\triangle O_2}{\triangle V} = \frac{V_G{}^2 + V_G V_L s_{CO_2} + V_L{}^2 s_{O_2} s_{CO_2}}{(1+Q) V_G{}^2 + V_G V_L s_{CO_2} + V_L{}^2 s_{CO_2} s_{CO}} \quad \text{(Fig. 25, curve 4)}$$

In the experiments (gas phase 1.7 % O_2, 3.3 % N_2, 93 % CO, 2 % CO_2; $V_G = 4.5$ ml): $\triangle O_2/\triangle V = 1.3^5$.

With the numerical values the parameters in the equations 4, 4a, 4b, 4c have under experimental conditions, it was discovered that $\triangle O_2/\triangle V$ is surprisingly insensitive to relatively large variations in these values, as can be shown by the substitution of slightly different numerical values for the parameters in the equation.

From the relative positions of curves 1 (20 % O_2, 80 % N_2, 2 % CO_2) and 2 (50 % O_2, 50 % N_2, 2 % CO_2), for instance, it is clear that a considerable change in the composition of the gas phase has no significant influence on $\triangle O_2/\triangle V$, if V_G is larger than 1 ml.

By means of equation 4a, 4b or 4c, according to the experimental conditions, the oxygen production $\triangle O_2$ can be calculated from the recorded volume change $\triangle V$. From $\triangle O_2$, which is expressed in volume units at prevailing temperature and atmospheric pressure minus water vapour pressure, the oxygen production was calculated in molar units according to well-known principles.

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A STUDY OF THE VEGETATION OF THE "TURFKOELE" AND OF THE PALYNOLOGICAL CHARACTER OF THE PEAT DEPOSITED IN THIS SWAMP

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(*'s Gravenzande*)

(*received September 1th, 1957*)

On the frontier of the municipalities "Melick en Herkenbosch" and "Vlodrop" near the road from Herkenbosch to boundery-mark 376, in the site named "Koezoep", in the province of Limburg, Netherlands, is a peat swamp, known as the "Turfkoele".

From the geological map (no. 58, fourth part sheet 4) it appears that the peat under the swamp has been formed on a deposit of river sand. This deposit has come from the Roer and lays on the middle terrace of this river and of the Meuse.

The swamp lies in a bend of the Roer valley. This bend, worn out in the low terrace of this river, consists of fine sand. So we may say that the peat has been formed in a deserted bend of the river Roer.

On three sides the surrounding soil lies about 5 meters above the surface of the swamp (+ 28 m N.A.P.). The edge, which I will call the "Hoge Wal" is on the north and east side of the swamp partly demolished, while on the south side the "Hoge Wal" has been planted with *Pinus sylvestris.*

The swamp is divided into a northern and a southern part by a regulated brook, the "Lange Graft", running from north-east to south-west and emptying into the Roer. The southern part of the "Turfkoele" receives water from the "Lange Graft" via a culvert. From this part rises a little brook, also emptying into the Roer.

In the northern part of the "Turfkoele" and on the edge nearby, borings have been made (boring C and A respectively), while boring B was made in the southern part.

First I will describe the present-day vegetation in a few words; after that the results of my palynological study of the peat. The latter will be compared with those of some peat studies carried out in other places, most of them in the neighbourhood.

VEGETATION OF THE SOUTHERN PART OF THE "TURFKOELE"

There is not much open water in this part. In the centre there is some, about 4 m deep, but for the greater part grown over with *Equisetum fluviatile.*

The water level changes after rainfall, especially in the *Alnetum* on the west side. In a dry period, it is possible to walk through this part in all directions, but after some days of rain, there may be more than 50 cm water. Undoubtedly this will influence the vegetation.

On the surface of it it looks as if this is the kind of vegetation typical for an oligotrophic soil, especially because of the abundance of *Myrica gale* and *Sphagnum* species. On closer examination this impression appears to be wrong. The part adjoining the "Lange Graft" has a vegetation characteristic for a eutrophic soil and consists of an *Alnetum-glutinosae* (with *Alnus glutinosa. Dryopteris austriaca*, *Humulus lupulus*, *Lysimachia vulgaris*, *Stachys palustris*, and other species), and a *Scirpeto-phragmitetum medio-europaeum* (with *Sparganium erectum*, *Typha latifolia*, *Scirpus sylvaticus*, *Stachys palustris* and others).

Along the "Hoge Wal" (on the south side) there is a narrow border consisting of a eutrophic vegetation, about 1.5 m broad, with a.o. *Alnus glutinosa*, *Solanum dulcamara*, *Calamagrostis canescens* and *Salix cinerea*. Probably the rain water sinks from the "Hoge Wal" as far as this border, which may explain its eutrophic character.

Going from this side to the middle of the swamp, first we see a *Caricion-fuscae* vegetation with much *Betula*, *Sphagnum* and some *Myrica*, an oligotrophic vegetation therefore. More to the centre this passes at various places into a *Scirpeto-phragmitetum medio-europaeum*. Only at one place we find a true peat moor with a vegetation belonging to the group of the *Ericeto-Sphagnetalia*, with *Sphagnum*, *Polytrichum*, *Eriophorum*, *Oxycoccus* and other species.

As mentioned before, on the west side of the swamp, there is an area with an eutrophic vegetation, first a *Querceto-carpinetum-filipenduletosum* (with a.o. *Alnus glutinosa*, *Filipendula ulmaria*, *Angelica sylvestris*, *Lysimachia vulgaris*, *Humulus lupulus*), passing into an *Alnetum-glutinosae*.

So we pass in the southern part of the swamp from a vegetation of *Equisetum fluviatile* (in the centre), via a trembling bog overgrown by *Typha latifolia* with *Cicuta virosa* and *Menyanthes trifoliata*, to *Sphagnum* societies of the *Caricion-fuscae* type, which in their turn pass into associations belonging to the group of the *Ericeto-Sphagnetalia*. The whole is surrounded by an oligotrophic vegetation consisting of *Myrica*, *Betula* and *Sphagnum* species except on the south side (narrow border of an eutrophic vegetation) and on the west side (*Alnetum-glutinosae*).

Vegetation of the northern part of the "Turfkoele"

This part is not so large as the southern one. The vegetation is of a meso- to eutrophic character. Along the southern border, the vegetation consists of an *Alnetum-glutinosae* with some transitions into a *Valerianeto-filipenduletum* (a.o. *Alnus glutinosa*, *Humulus lupulus*, *Stachys palustris*, *Cicuta virosa*, *Scirpus sylvaticus*, *Solanum dulcamara*). Towards the centre are transitions into a *Caricion-fuscae* too (a.o. *Sphagnum contortum*, *Sphagnum subsecundum*).

Going from the north side to the centre, first we find a *Phragmition-eurosibiricum* with a *Valerianeto-filipenduletum* (a.o. *Typha latifolia*, *Sphagnum molle*, *Equisetum fluviatile*, *Lysimachia vulgaris* and *Stachys* *palustris*), passing into a *Valerianeto-filipenduletum* with an *Alnion-glutinosae* and a *Caricion-fuscae* vegetation.

From the north side a narrow "ridge" runs into the swamp. On this ridge we find an *Alnetum-glutinosae*, passing at the border into a *Valerianeto-filipenduletum.*

Open water is found only in the western part. Round it grows *Equisetum fluviatile*, and this vegetation passes into a *Valerianeto-filipenduletum*, *Scirpeto-phragmitetum medio-europaeum* and, locally, into a *Caricion-fuscae* and an *Alnetum-glutinosae* vegetation.

The surface is not so densely covered with *Sphagnum* as in the southern part of the swamp. Furthermore, there are more trees in this part, especially *Alnus glutinosa* and some *Betula pubescens*; relatively little *Myrica gale.*

So we find in the northern part a vegetation with *Equisetum fluviatile* (only in deeper water) passing into a *Scirpeto-phragmitetum medio-europaeum*, *Caricion-fuscae* and a *Valerianeto-filipenduletum*; locally also into an *Alnetum-glutinosae*, especially on the northern and southern border of this part of the swamp.

PALYNOLOGICAL ANALYSIS OF THE PEAT

Boring A

Palynological Aspect

From the Fig. 1 it appears that the lowermost layer contains many pollen grains of *Pinus*, less of *Betula* and *Salix*. The herb-pollen percentage too is rather low. So the first peat must have been formed during the Praeboreal. First, the pollen percentage of *Pinus* fluctuates round 60 %, but after the appearance of *Corylus*, and then of *Alnus*, this percentage decreases rapidly. At 1.80 m thermophilous trees appear. The pollen percentage of these trees increases very fast, so at 1.80 we may locate the boundary line between Praeboreal and Boreal. In the Boreal we see a slight indication of a *Corylus* top (23 %). *Alnus* appears at a depth of 1.70 m. At first the percentage remains under 10 %, but higher on it increases (from 1.10 m).

At 1.50 we meet the Quercetum mixtum, at first *Ulmus* only, after that *Tilia* and *Quercus* too. The *Alnus*-pollen percentage increases fast and at 0.90 m the *Alnus* and *Pinus* lines cross each other. This is the beginning of the Atlanticum.

In the Atlanticum the *Corylus*, *Alnus* and Quercetum-mixtum lines rise further. At 0.70 m the Quercetum mixtum has a top in the Atlanticum (29 %), caused by *Quercus* (15 %), *Tilia* (7 %) and *Ulmus* (7 %). After this the Quercetum-mixtum percentage decreases. This decrease, together with a maximum of Corylus (32,5 %), indicates the boundary line between Atlanticum and Subboreal (0.60 m). The low percentage of Ericaceous pollen increases slightly too. The Quercetum mixtum has been partly pushed aside by *Corylus*, which reaches a maximum in the Subboreal. After this the *Corylus* percentage also decreases.

At 0.30 m *Fagus* and pollen grains of cultivated *Gramineae* appear.

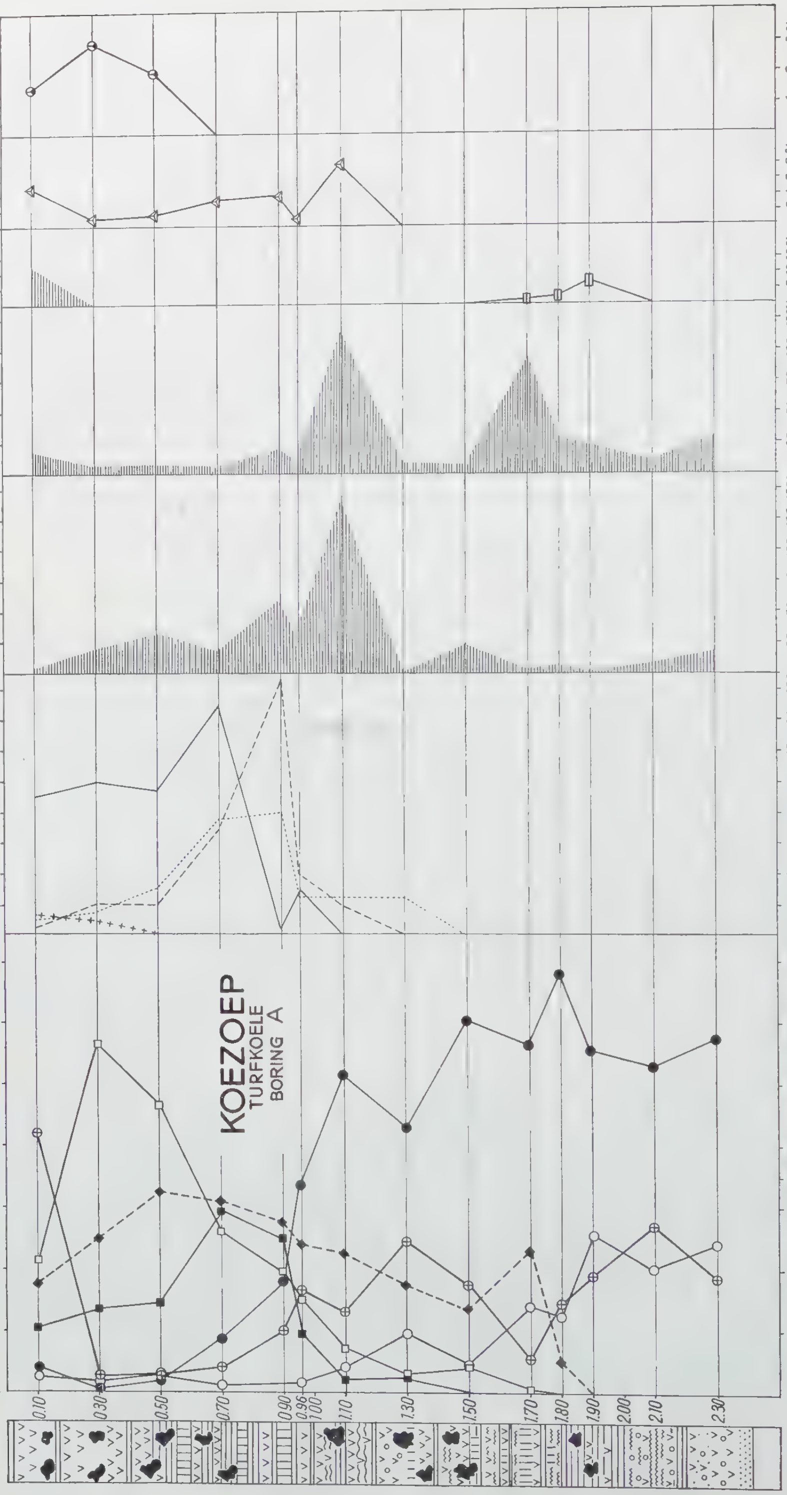
ERICACEAE
1 2 3%
SPHAGNUM
2 4 6 8%
CEREALIA
ARTEMISIA
5 10 15%
GRAMINEAE+CYPERACEAE
25 50 75 100 125%
FILICES
25 50 75 100 125 150%
QUERCETUM MIXTUM
0 2 4 6 8 10 12 14 16%
0 10 20 30 35 40 50 60 70%
KOEZOEP
TURFKOELE
BORING A
0.10
0.30
0.50
0.70
0.90
0.96
1.00
1.10
1.30
1.50
1.70
1.80
1.90
2.00
2.10
2.30

Fig. 1

Alnus reaches a maximum (56 %); the *Salix* percentage increases suddenly to 42 %, pointing to a *Salicetum* in accordance with the present day vegetation.

The *Fagus*-pollen percentage remains very low which suggests that the Subatlantical peat has been removed and eventually has been replaced in the upper layers of the deposit by recent peat.

Stratigraphical Aspect

It appears that the peat rests on river sand mixed with fine gravel. The lowest peat layers contain much wood and fruits of *Betula*. Probably there was a *Betula-Salix* marsh here, with *Pinus* in the surrounding country. The undergrowth consisted of *Filices* and *Gramineae* with some *Musci*. After this the water level rose a little, for besides the *Gramineae* at the lower level, *Carex*, *Eriophorum*, *Phragmites* and *Sphagnum* appear. In the surroundings the conifers (*Pinus*) were replaced by deciduous trees (*Quercus*, *Tilia* and *Corylus*).

The upper peat layers consist of a woody peat, with *Carex* and some *Ericaceae*. The vegetation of these peat layers will have resembled the present-day vegetation to a large extent.

So, the whole gives the impression of a marsh, at one time drier than at other times.

Boring B

Palynological Aspect

As in boring A, *Pinus* (50 %), *Betula* (28 %) and *Salix* (16 %) appear first in Fig. 2. The herb-pollen percentage is low, so the peat had been formed first in the Praeboreal.

At 1.70 m *Pinus* reaches a maximum (76 %) but decreases rapidly. *Betula* and *Salix* fluctuate round 23 %, resp. 10 %.

In the diagram we see *Corylus* and *Alnus* appear at 1.50 m. The pollen percentages of these trees rise fast and at 1.50 m the boundary line between Praeboreal and Boreal is reached. At the same time the Quercetum mixtum, with *Quercus* and *Tilia*, makes its appearance.

Here, too, *Corylus* reaches a just perceptible top in the Boreal (22,5 %).

The crossing of the *Pinus* and *Alnus* lines takes place at about 1.20 m, this being the beginning of the Atlanticum. At the same time the Quercetum mixtum reaches a maximum (19.5 %) caused by *Quercus* and *Tilia*.

Here, either the growth of the peat must have stopped for a time; or a peat layer has been washed away. This seems the more plausible as a deposit of river sand is found here. Hence, this part of the diagram is not wholly reliable.

After the crossing of the *Pinus* and *Alnus* line, the *Corylus* percentage increases and then declines. At this moment there is an *Ericaceae* maximum too, though of less significance. The Quercetum-mixtum percentage drops too. Conclusion: this part belongs to the Subboreal (from 1.10 m).

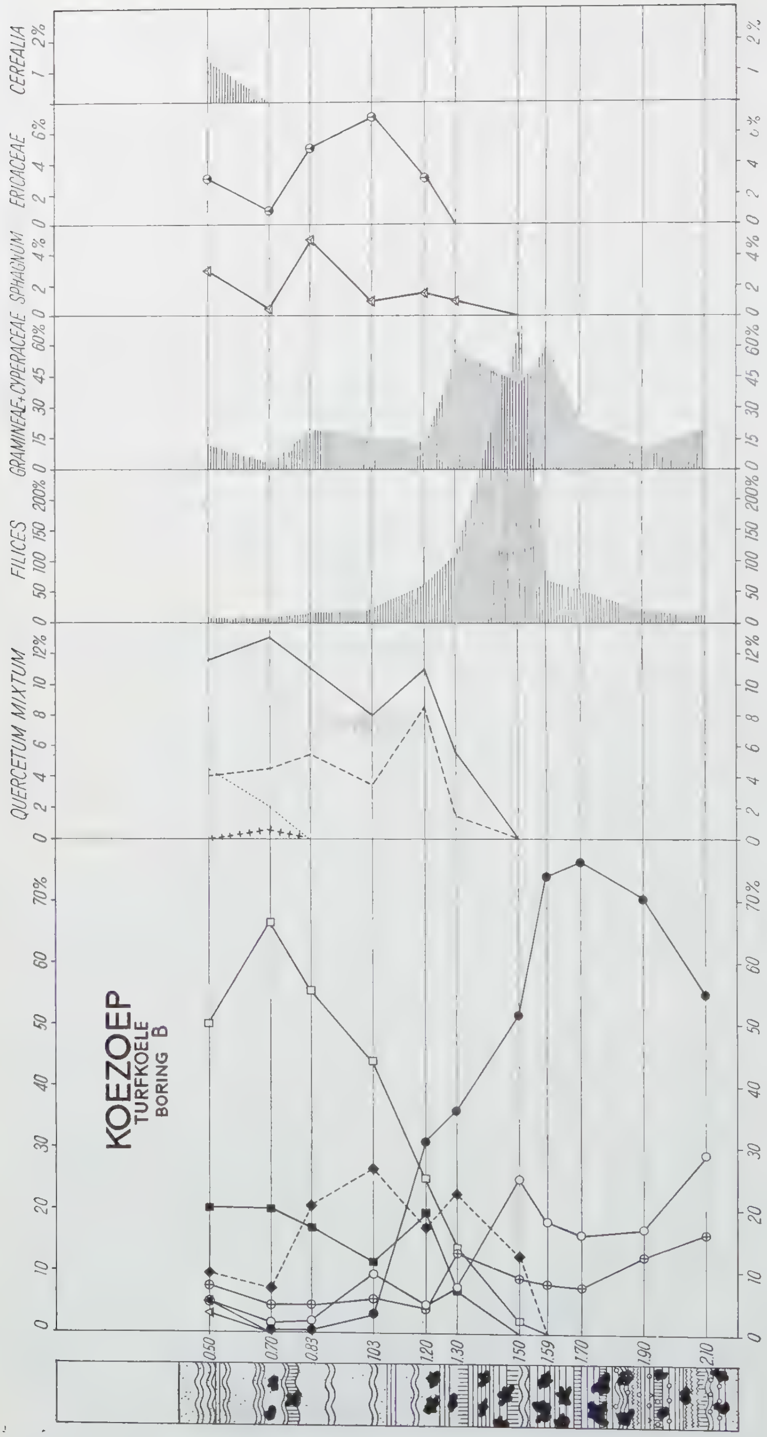
KOEZOEP
TURFKOELE
BORING B
CEREALIA
1
2%
ERICACEAE
0
2
4
6%
SPHAGNUM
0
2
4%
GRAMINEAE+CYPERACEAE
0
15
30
45
60%
FILICES
0
50
100
150
200%
QUERCETUM MIXTUM
0
2
4
6
8
10
12%
0
10
20
30
40
50
60
70%
0.50
0.70
0.83
1.03
1.20
1.30
1.50
1.59
1.70
1.90
2.10

Fig. 2

Above 0.70 m we see *Fagus* and *Carpinus*, together with cultivated *Gramineae*, and an *Alnus* top (66 %) as in boring A.

Stratigraphical Aspect

Here again, the peat appears to rest on a deposit of river sand. The undermost layers are built up in a *Betula-Salix* marsh, with *Carex*, *Sphagnum*, *Eriophorum* and *Phragmites*, with *Pinus* in the immediate surroundings.

As far as about 1.20 m the structure of the peat does not change much. Then we find river sand again, brought probably by the Roer, with a little *Sphagnum* and *Carex*, higher up with *Phragmites*. Up to the upper layers the peat remains very sandy. On the peat we find circ. 50 cm water with *Sphagnum* growing in it.

Boring C

Palynological Aspect

At first, the spectra (Fig. 3) show a high percentage of *Pinus* pollen (78.5 %) and some of *Betula*, *Salix* and various herbs (at first some *Gramineae* and *Cyperaceae*, but these disappear soon). Here too, peat must have been formed from the Praeboreal. At 2.15 m we see thermophilous trees, all appearing at the same time and their pollen percentages increase fast. Therefore, it is impossible to give a good classification.

At about 1.80 m there are pollen grains of *Fagus* and *Carpinus*. As in boring A, cultivated *Gramineae* are found together with *Fagus* in the top layers. It looks as if the peat has partly been removed by dredging. The lowermost layers have not been disturbed. The upper peat may have been formed in recent times; the intermediate layers would have been removed. The *Alnus* maximum, at the top of the deposit, points to a vegetation corresponding to that of the present day.

Stratigraphical Aspect

Here again, the peat rests on a deposit of river sand. The undermost layers are built up in a *Betula-Salix* marsh, with *Sphagnum*, *Eriophorum* and some *Carex*, with *Pinus* in the immediate surroundings. The uppermost layers are mixed with river sand and are built up with *Carex*, *Eriophorum* and *Phragmites*.

Comparison of the borings

Palynological Aspects

In the "Turfkoele" the first peat was formed in the Praeboreal; it contains many pollen grains of *Pinus* and some of *Betula* and *Salix*. From the thermophilous trees we see first *Corylus*, followed by, or appearing at the same time with *Alnus*. Then the Quercetum mixtum appears, with *Quercus* and *Tilia* chiefly. In the Boreal there is an indication of a *Corylus* top. After the crossing of the *Pinus* and *Alnus* lines in the diagram, the Quercetum mixtum reaches a maximum,

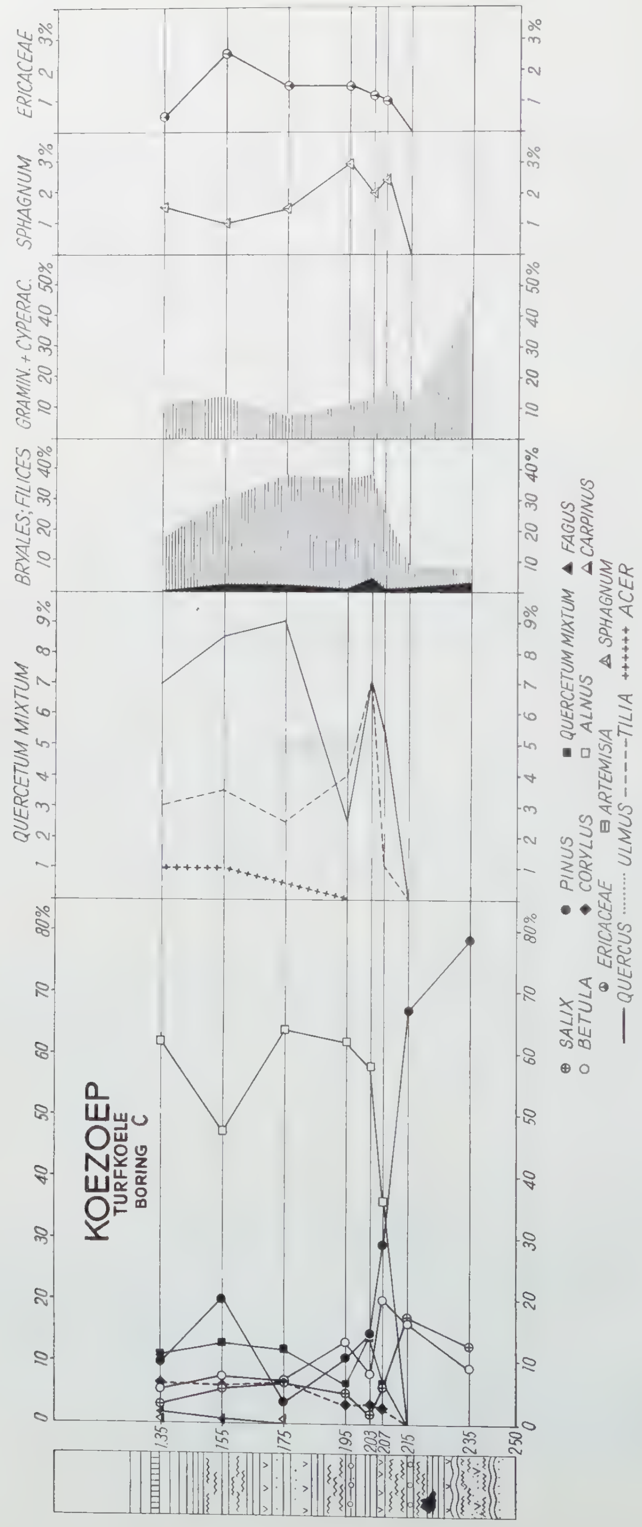
KOEZOEP
TURFKOELE
BORING C
135
155
175
195
203
207
215
235
250
0
10
20
30
40
50
60
70
80%
QUERCETUM MIXTUM
1 2 3 4 5 6 7 8 9%
BRYALES; FILICES
10 20 30 40%
GRAMIN. + CYPERAC.
10 20 30 40 50%
SPHAGNUM
1 2 3%
ERICACEAE
1 2 3%
⊕ SALIX
○ BETULA
⊕ ERICACEAE
● PINUS
◆ CORYLUS
⊞ ARTEMISIA
■ QUERCETUM MIXTUM
□ ALNUS
△ SPHAGNUM
▲ FAGUS
△ CARPINUS
—— QUERCUS
.... ULMUS
– – – – TILIA
+++++ ACER

Fig. 3

which in diagram B is probably secondary. In the subboreal the Quercetum mixtum was pushed aside by *Corylus;* the latter reaches a maximum here.

Stratigraphical Aspects

From the three borings we may conclude that the peat was formed upon river sand deposited by the Roer. The undermost layers were built up in a *Betula-Salix* marsh with an undergrowth, and with *Pinus* in the immediate surroundings. Afterwards *Pinus* was pushed aside by deciduous trees.

From the borings B and C it becomes clear that at the end of the Subboreal the Roer again deposited river sand. To do so, the Roer had to change its course. After another diversion of the river bed the peat bog remained very wet (borings B and C).

In boring B we find first a wet marshy peat, above it a peat built up with *Carex* and *Sphagnum.* In boring C we find the same, with *Carex*, *Phragmites* and *Eriophorum;* in boring A we have to deal with a marshy peat becoming gradually dry.

In comparing the diagrams with those of H. J. Eshuis (1946): the southern Peel (profile 5 of Eshuis), we find a marked difference in the age of the peat; that in the "Turfkoele" being older, namely Praeboreal, in opposition to the Boreal or Atlantic age of the peat in the southern Peel. After the crossing of the *Pinus* and *Alnus* lines the percentage of the *Pinus* pollen-grains remains low in both diagrams. In the diagram of Eshuis, *Corylus* has a top in the Atlanticum-Subboreal, so somewhat earlier than in the "Turfkoele". The same applies to *Alnus*, this reaching a top in the Subboreal in the Peel. In both peat formations we find a Quercetum-mixtum top in the Atlanticum caused by *Quercus* chiefly. In the diagram of the southern Peel we see *Fagus* in the beginning of the Atlanticum. In the "Turfkoele" only the upper layers contain a few *Fagus* pollen-grains.

It is impossible to compare the palynological character of the peat near Susteren (L.), studied by Florschütz (1941), with that of the "Turfkoele". There the peat is chiefly of late-glacial age and it was apparently dug off above the crossing of the *Pinus* and *Alnus* lines.

Nearer to the "Turfkoele" is the peat bog near Broeksittard (L.) studied by Belderok and Hendriks (1951). In comparing their diagram with those of the "Turfkoele" we see in both diagrams a *Corylus* maximum in the Boreal and a Quercetum-mixtum top in the Atlanticum, caused by *Quercus* and some *Tilia* and *Ulmus.* At the transition of the Subboreal into the Subatlanticum there is an *Alnus* top. Remarkable is the fact of thermophilous trees appearing already in the Late-glacial and early Praeboreal. Belderok en Hendriks do not mention this fact.

The diagrams of the "Turfkoele" as well as those of the "Hautes Fagnes" (van der Hammen, 1951: "Belle Croix"; Florschütz and van Oye, 1939: "Vivier Fagnoul") and of the border of the Eiffel (Persch, 1950), so the pollen diagrams of peat bogs of the southern

Netherlands and the adjoining parts of Belgium and Germany, are characterized by an, on the whole, intensive development during the Praeboreal. There is no regularity in the arrival of thermophilous trees. In the northern Netherlands and Denmark, *Corylus* appears first, mostly in the young Praeboreal; after that come *Ulmus* and *Quercus;* and *Alnus* and *Tilia* only in the second part of the Boreal. In the south this is not common. Here the thermophilous trees often appear all at the same time. Among the components of the Quercetum mixtum, the large percentage of *Tilia* is striking. At the same time with, or preceding the maximum extension of the Quercetum mixtum (Atlantic Quercetum-mixtum top) we find an, often rather high, maximum of *Tilia.*

In the diagrams of the "Turfkoele" the relative low percentages of *Corylus* during the Boreal are striking.

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KWALITATIEVE EN KWANTITATIEVE VERANDERINGEN IN DE BOTANISCHE SAMENSTELLING VAN EEN DUINGRASLAND GEDURENDE EEN VEGETATIEPERIODE

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(*ingekomen 13 augustus 1957*)

Het is bekend dat van het bovengronds aanwezige deel van een vegetatie zowel de samenstelling als de onderlinge massaverhouding der soorten gedurende de groeiperiode aan sterke wijzigingen onderhevig is. In de zoölogie kent men een analoog verschijnsel, dat daar als ,,populatiedynamiek" bekend staat. In de vegetatiekunde wordt het dynamisch aspect echter gewoonlijk met iets anders in verband gebracht, n.l. met de gerichte veranderingen in soortensamenstelling, die tenslotte tot het ontstaan van een andere plantengemeenschap kunnen leiden en die samenhangen met geleidelijke milieuveranderingen (successie). De veranderingen in een vegetatie, die verband houden met de groeiperiodiciteit der soorten, zijn cyclisch van karakter en men zou hier in tegenstelling tot de successie van seizoendynamiek kunnen spreken.

In de fenologie worden bepaalde facetten van de seizoendynamiek bestudeerd (uitlopen van knoppen, eerste bloei, zaadrijping, enz.) en in verband gebracht met klimatologische omstandigheden. Kwalitatieve waarnemingen in deze zin vindt men reeds in de oudere literatuur. Zo deelde MASSART (1908) de planten van de Belgische duinkust in naar de tijd van kieming, bladontwikkeling, bloei en zaadvorming en naar hun totale levensduur in de vegetatiecyclus. In latere tijd beschreef ELLENBERG de ,,symfenologie" van *Querceto-Carpinetum* en *Querceto-Betuletum* (1939; overgenomen in MELTZER en WESTHOFF, 1944) en van het Arrhenatheretum (1952; zie ook ELLENBERG, 1956). In ELLENBERG (1954) wordt naar een meer kwantitatieve weergave van fenologische verschijnselen gestreefd.

De studie van de seizoendynamiek moet uit verschillend oogpunt van belang geacht worden. Primair geeft zij ons een inzicht in de gedragingen van de soorten over het jaar en ligt zij dus op het terrein van de fenologie. Wordt het onderzoek over een aantal jaren voortgezet, dan zal ons dit in staat stellen de ontwikkeling van de soorten in verband te brengen met de weersgesteldheid, terwijl uitbreiding van het onderzoek over verscheidene vegetatietypen naar alle waarschijnlijkheid conclusies met betrekking tot de invloed van het biotoop mogelijk zal maken. Omgekeerd kunnen fenologische waarnemingen aanwijzingen geven ten aanzien van bepaalde klimaatsfactoren (Ellenberg, 1954).

Daarnaast kan de studie van de seizoendynamiek van nut zijn bij andere vegetatiekundige arbeid. In het algemeen verschaft zij een basis, waarop vegetatieopnamen, die niet gelijktijdig of op overeenkomstige tijdstippen gemaakt worden, onderling vergeleken kunnen worden. O.a. is dit van belang bij de verwerking van een aantal vegetatieopnamen in een tabel. Bij de berekening van de presentie van een soort binnen het onderhavige vegetatietype is het — indien men over gegevens ten aanzien van de seizoendynamiek beschikt — mogelijk die opnamen uit te sluiten, welke gemaakt werden op een tijdstip, waarop de betrokken soort in het algemeen in dit vegetatietype nog niet waar te nemen of reeds verdwenen is. Wanneer men bovendien een waarde wenst op te geven voor de abundantie, bedekking of sociabiliteit, waarmee een soort in de vegetatie aanwezig pleegt te zijn — zoals dat in zg. verkorte tabellen toepassing vindt — zou men zich hierbij in plaats van op de reële opnamen kunnen funderen op de hieruit door „extrapolatie'' verkregen hypothetische opnamen. De opnamen der verschillende vegetaties, gemaakt op verschillende tijdstippen zijn nl. in principe niet onderling vergelijkbaar en zouden derhalve in dit geval vervangen moeten worden door de afgeleide opnamen, die wel op hetzelfde tijdstip betrekking hebben en dus gelijkwaardig zijn. Men zal voor dit laatste tijdstip in het algemeen dat van de optimale ontwikkeling der vegetatie kiezen, hetgeen echter voor ieder geval afzonderlijk nader gepreciseerd moet worden. Dat aan deze methode gevaren verbonden zijn zal niet ontkend worden, maar het lijdt geen twijfel, dat langs deze weg een juistere en scherpere karakterisering van het vegetatietype verkregen kan worden.

Ook bij het successieonderzoek, dat hier te lande de laatste jaren een steeds grotere plaats in de studie der vegetatie gaat innemen, zal men er niet steeds in slagen de hierbij vereiste periodiek herhaalde opname der proefperken op volkomen overeenkomstige tijdstippen te laten plaats vinden. Bij de interpretatie der verschillen in de vegetatie zijn gegevens omtrent de seizoendynamiek wel haast onontbeerlijk.

Een practische moeilijkheid doet zich bij het onderzoek der seizoendynamiek gevoelen: uiteraard is men n.l. gedurende een gehele vegetatieperiode aan het terrein van onderzoek gebonden. Het onderzoek verliest aan waarde indien men een langer aaneengesloten tijdvak afwezig is.

Sinds 1951 houdt de auteur zich o.a. bezig met de bestudering van de vegetatie van het duingebied der Haagse Duinwaterleiding.

In de zomer van 1956 heeft hij zich van eind april tot medio augustus zonder noemenswaarde onderbreking aan deze studie kunnen wijden, zodat zich een goede gelegenheid voordeed een onderzoek naar de seizoendynamiek van een bepaalde vegetatie aan te vangen.

Daartoe werd een zeer homogeen grasland uitgekozen, gelegen in een beschutte duinpan enige km ten noordoosten van Scheveningen (ca. 600 m van het strand af ter hoogte van strandpaal 95). In syn-systematisch opzicht behoort de vegetatie tot het *Koelerion albescentis* (Br.-Bl.) Weevers 1940. Elders zal dit vegetatietype beschreven worden als *Taraxaco-Galietum plantaginetosum*. Een deel van het graslandje, groot 7,7 m², werd gemarkeerd en in totaal tien maal opgenomen: voor het eerst op 26/4–1956 en vervolgens op 2/5, 14/5, 22/5, 12/6, 25/6, 17/7, 25/7, 8/8, en 6/10. Voor een dergelijk onderzoek, waarbij de onderlinge massaverhouding der soorten zo nauwkeurig mogelijk genoteerd dient te worden, verdient het in het algemeen aanbeveling bij de waardering van abundantie en bedekking van de decimale schaal gebruik te maken (DOING KRAFT, 1954). In dit geval liet de struktuur van de vegetatie evenwel geen schattingen tot op tienden toe, zodat de door BRAUN–BLANQUET (1928, 1951) voorgestelde schaal toegepast werd.

In de figuur werden van alle in de proefvlakte aangetroffen hogere planten de op de genoemde data toegekende waarden voor gecombineerde schatting op schaal uitgezet. Ook de horizontale indeling geschiedde op schaal, met uitzondering van het laatste tijdvak (8/8–16/10). Bovendien werd de bloeiperiode van de betrokken soorten aangegeven.

Aangezien de details uit de figuur af te leiden zijn, kan met de volgende opmerkingen worden volstaan:

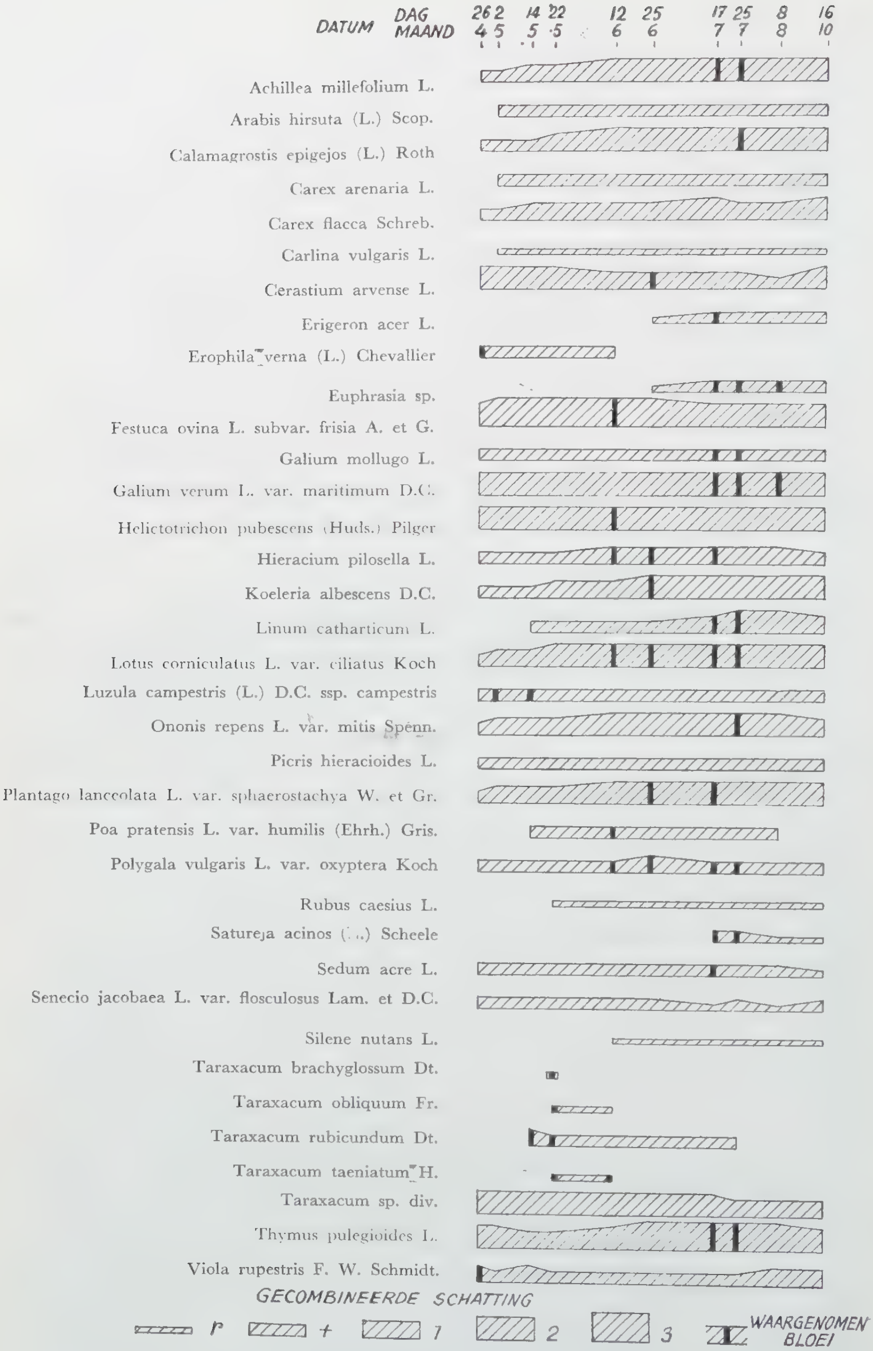
1. Soorten met een relatief hoge bedekkingsgraad geven in de lente en voorzomer een toename in bedekking te zien, die pas in de late herfst of winter door een afname wordt gevolgd.

2. Een uitzondering hierop maken o.a. *Helictotrichon pubescens* en *Galium verum*, die gedurende de gehele vegetatieperiode min of meer konstant blijven.

3. Afwijkend zijn voorts *Cerastium arvense* en *Thymus pulegioides*. *Cerastium arvense* neemt af gedurende de voorzomer, bereikt midden in de zomer een dieptepunt en neemt in de herfst weer duidelijk toe. Ook *Thymus pulegioides* neemt aanvankelijk af (gevolg van concurrentie van andere soorten, die juist in deze periode een sterke uitbreiding vertonen?), maar wijst reeds in de voorzomer een toename aan en bereikt midden in de zomer zijn maximum.

4. Soorten, die slechts weinig of sporadisch voorkomen kunnen uiteraard geen grote veranderingen in abundantie demonstreren. Van groter belang is hier het tijdstip, waarop de soort voor het eerst, eventueel voor het laatst werd waargenomen, hoewel juist hier het gevaar bestaat, dat de soort aanvankelijk een keer over het hoofd werd gezien. Opvallend is het late verschijnen van *Rubus caesius*, *Silene nutans*, *Erigeron acer*, *Euphrasia sp.* en *Satureja acinos* (zie echter 5).

5. Het is gebleken, dat men er niet steeds in slaagt iedere subjectiviteit bij de schattingen van abundantie en bedekking uit te sluiten. Door de struktuur van de vegetatie is het voor enkele weinig opvallende soorten bijvoorbeeld zeer moeilijk alle individuen in de schatting te betrekken en krijgt men pas een volledig overzicht van hun voorkomen wanneer zij bloeien. Er bestaat daardoor een neiging sommige soorten tijdens de bloei hoger te waarderen. Ook is het niet uitgesloten, dat een psychologische faktor hierbij een zekere rol speelt.


DATUM
DAG MAAND
26 4
2 5
14 5
22 5
12 6
25 6
17 7
25 7
8 8
16 10
Achillea millefolium L.
Arabis hirsuta (L.) Scop.
Calamagrostis epigejos (L.) Roth
Carex arenaria L.
Carex flacca Schreb.
Carlina vulgaris L.
Cerastium arvense L.
Erigeron acer L.
Erophila verna (L.) Chevallier
Euphrasia sp.
Festuca ovina L. subvar. frisia A. et G.
Galium mollugo L.
Galium verum L. var. maritimum D.C.
Helictotrichon pubescens (Huds.) Pilger
Hieracium pilosella L.
Koeleria albescens D.C.
Linum catharticum L.
Lotus corniculatus L. var. ciliatus Koch
Luzula campestris (L.) D.C. ssp. campestris
Ononis repens L. var. mitis Spenn.
Picris hieracioides L.
Plantago lanceolata L. var. sphaerostachya W. et Gr.
Poa pratensis L. var. humilis (Ehrh.) Gris.
Polygala vulgaris L. var. oxyptera Koch
Rubus caesius L.
Satureja acinos (L.) Scheele
Sedum acre L.
Senecio jacobaea L. var. flosculosus Lam. et D.C.
Silene nutans L.
Taraxacum brachyglossum Dt.
Taraxacum obliquum Fr.
Taraxacum rubicundum Dt.
Taraxacum taeniatum H.
Taraxacum sp. div.
Thymus pulegioides L.
Viola rupestris F. W. Schmidt.
GECOMBINEERDE SCHATTING
r
+
1
2
3
WAARGENOMEN BLOEI

Zo is het mogelijk, dat bij *Polygala vulgaris* (volle bloei op 25/6) en *Linum catharticum* (volle bloei 25/7) voorafgaande en latere schattingen (relatief) iets te laag zijn uitgevallen. Behalve als fenologisch gegeven en eventueel als maatstaf voor de vitaliteit is het dus ook uit dezen hoofde gewenst in een opname te vermelden welke soorten in bloei staan. Een extreem geval deed zich voor bij *Satureja acinos*, welke soort pas waargenomen werd toen zij in bloei kwam (17/7); deze soort moet reeds tijdens voorgaande opname(n?) boven de grond geweest zijn.

6. De achtereenvolgens voor de *Taraxacum*-soorten toegekende waarden behoeven eveneens een toelichting. Wel werden hiervan de afzonderlijke individuen steeds waargenomen, maar een determinatie van de soort was slechts mogelijk tijdens de bloei en eventueel gedurende enige tijd daarna. Het grootste deel der planten kwam niet tot bloei en was dienovereenkomstig niet met zekerheid te determineren.

Het is duidelijk, dat om het gedrag van verschillende soorten binnen een plantengemeenschap na te gaan het wenselijk is niet alleen meerdere proefperken in het onderzoek te betrekken maar dit ook uit te strekken over enige jaren. Zo heeft de koude en natte zomer van 1956 in het algemeen tot een weelderiger ontwikkeling van de droge duingraslanden geleid. Omtrent de invloed van koudere of warmere, vochtiger of droger jaren en over een korter tijdsbestek de invloed van de weersgesteldheid valt echter pas meer te zeggen wanneer het onderzoek over een aantal jaren voortgezet wordt.

Bovendien zou het onderzoek aan nauwkeurigheid winnen indien van soorten, die zich hiertoe lenen, niet hun abundantie geschat, maar het aantal individuen — eventueel op een veel kleinere proefvlakte begrepen — geteld werd.

Om praktische redenen moest het onderzoek zich tot de geschetste gang van zaken bepalen.

ZUSAMMENFASSUNG

Die Entwicklung eines Dünengraslandes, *Koelerion albescentis* (Br.-Bl.) Weevers 1940, während einer Vegetationsperiode wurde studiert. Im allgemeinen zeigen die Arten eine Zunahme der Bedeckung oder Abundanz im Frühling und Frühsommer, während eine deutliche Abnahme erst im Spätherbst oder Winter erfolgt. Abweichend vom Typus sind: *Helictotrichon pubescens*, *Galium verum*, *Cerastium arvense* und *Thymus pulegioides* (siehe Figur). Verschiedene Arten wurden im Frühsommer zum ersten Mal beobachtet. Der kalte Frühling und der nasse Sommer des Jahres 1956 dürften gewisse Verschiebungen verursacht haben.

Ontwikkeling van het *Taraxaco-Galietum* gedurende een vegetatieperiode (1956).

Bovendien kwamen in de proefvlakte de volgende Kryptogamen en Lichenen voor (tussen haken de datum waarop de soort voor het eerst werd waargenomen): *Bryum capillare* L. (2/5) +; *Camptothecium lutescens* B. et S. (25/7) r; *Hypnum cupressiforme* L. var. *elatum* B. et S. (26/4) 3; *Lophocolea bidentata* (25/7) +; *Mnium affine* Bland. (26/4) +; *Tortella flavovirens* (2/5) +; *Cladonia rangiformis* Hffm. var. *muricata* (Del.) Arn. (26/4) 3; *Cladonia furcata* (Hds.) Schrad. var. *racemosa* (Hffm.) Flk. (26/4) +; *Peltigera canina* (L.) Willd. (8/8) r.

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A NEW GENUS OF LINDSAEOID FERNS

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(*received May 16th, 1957*)

In revising the New World representatives of the genus *Lindsaea*, the author came across a fern specimen from Borneo preserved in the Rijksherbarium, Leiden, that did not seem to fit into any described genus. It had been described as *Schizoloma stortii* v. A. v. R., but in the author's opinion the genus *Schizoloma* Gaud., typified by *Lindsaea ensifolia* Sw., cannot be maintained (Kramer, 1957). Almost all species that in modern works have been left in it (e.g. Holttum, 1954; Alston, 1956, as *Schizolegnia*) should be put back in *Lindsaea*. This, however, cannot be done with *Sch. stortii*, as this species possesses a peculiar combination of characters unlike anything found in *Lindsaea*. Its pinnae have a median main vein as in *L. ensifolia*, but are free-veined, and they have a large basal acroscopic auricle as in *Isoloma*, but are non-articulate. There is a remote resemblance to *Lindsaea walkerae* Hook., which may be its closest relative, as stipulated by van Alderwerelt van Rosenburgh in his original description; the natural place of that species too would perhaps be in a separate genus. *Sch. stortii* differs from it, a.o., by its pale axes and alternate auriculate pinnae. Because of its apparently rather isolated position, it seems indicated to create a separate genus for this fern.

Xyropteris Kramer, genus novum. — Ex affinitate Lindsaeae et Isolomae, exstat petiolo rhachideque pallida, pinnis alternis exarticulatis praeter auriculam basalim acroscopicam aequilateralibus, venis liberis, soris continuis. (Name derived from Greek *ξυρόν*, razor-blade). Type and only species:

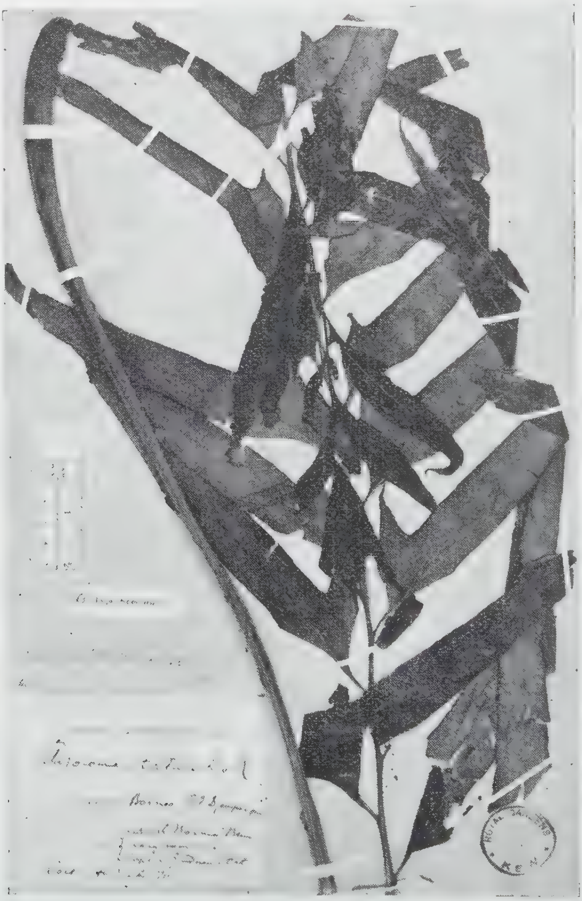
Xyropteris stortii (v. A. v. R.) Kramer, comb. nov.

Basionym: *Schizoloma stortii* v. A. v. R., Bull. Jard. Bot. Buitenz. 2me sér. 16:36 (1914); Malayan Ferns and Fern Allies Suppl. 1:214 (1916).

Schizolegnia stortii (v. A. v. R.) Alston, Bol. Soc. Broter. 2a sér. 30:24 (1956).

The original description, of which an almost verbal translation into English appeared two years later in the second of the above-named publications, is rather short and very incomplete, which is probably why this peculiar fern has never drawn the attention of other Pteridologists. Therefore a more complete description is given.

Rhizome apparently short-creeping (only short pieces present), stout, ca. 1¼ cm in diam., solenostelic; scales lanceolate, acuminate, evenly golden-brown, non-clathrate, up to 5 mm long and 1.5 mm wide, with up to ca. 18 rows of cells at the base; similar scales persistent on the base of the petiole. *Stipes* stramineous to fawn-coloured, terete at the base, upwards gradually channelled on the adaxial side, striate-canaliculate when dry, very stout, up to 1 ½ cm in diam. at the base, 70 cm long, with a single vascular bundle. *Rachis* similar, adaxially with a narrow groove, its margins not interrupted at the insertion of the pinnae. *Lamina* up to ca. 1 ½ m long, apparently broadly lanceolate, chartaceous to subcoriaceous, dark olivaceous on the adaxial side, paler on the abaxial side, simply pinnate. *Pinnae* up to ca. 20 on each side, alternate, rather remote, the basal ones over 20 cm apart, the upper ones gradually closer, ascending under an angle of ca. 40°, provided with an adaxially sulcate stalk up to 1 cm long, and up to 30 cm long and 3 cm wide, narrowly lanceolate, the largest ones 7 to 10 times as long as wide, the upper ones relatively wider; lower pinnae not reduced, the upper



ones gradually smaller, the uppermost ca. 8 cm long, subsessile; terminal segment distinct, trilobed (lost or damaged in all specimens). Base of pinnae long-cuneate, the leaf-tissue more strongly cut away on the basiscopic side, the acroscopic side at the base with a large acute auricle up to 7 cm long, either parallel with or somewhat divergent from the rachis; apex acuminate, coarsely serrate, the teeth ca. 1 cm apart; barren apex of auricle also serrate. Main vein median, raised on both sides, grooved on the adaxial side, stramineous to fawn-coloured; veins immersed but readily visible, very oblique, departing under an angle of ca. 10° from the midrib but less oblique towards the margin, free except as united by the receptacle, mostly two or three times forked; the basal auricle also with a main vein. *Sori* continuous, absent from the extreme base and apex of the pinnae and the apex of the auricle. Indusium linear, opening outwardly, entire or wavy, brown, 0.25–0.30 mm wide, falling short of the margin by approximately its own width, more or less reflexed at full maturity. Sporangia ca. 280 × 210 μ; annulus with 16-18 indurated cells which reach the insertion of the stalk; stomium strongly indurated, consisting of ca. 6 cells. Sporangia intermingled with filiform ca. 250 μ long paraphyses of 5 to 6 cells with brown, apparently glandular apex. Spores medium brown, smooth, monolete, bean-shaped, 30 × 50 — 35 × 60 μ, probably 16 per sporangium.

Distribution: Only known from type-collection: Amdjah 711 (Captain van Genderen Stort's collector) from Mt. Djempanga, Borneo (B,O HOLOTYPE, 2 sheets; Isotypes in K, 2 sheets, L; fragment and sketch in C. Chr. in BM).

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HEPATIQUES DU SURINAM

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(*reçu le 14 septembre, 1957*)

Il n'existe pas, actuellement, de catalogue des Hépatiques du Surinam. Les Hépatiques de ce pays restent très peu connues. Cependant, certaines ont attiré l'attention des Bryologues et ont été citées dans quelques ouvrages anciens ou récents. Je ne ferai pas ici une révision complète de ces publications, mais je crois utile de noter les principales:

1. C. Montagne, Seconde centurie de plantes cellulaires exotiques nouvelles, Ann. Sc. Nat., 1841, p. 71. – Les espèces suivantes, récoltées par Splitgerber, sont signalées: *Plagiochila serrata* Lindb., *P. hypnoides* Lindb., *Phragmicoma surinamensis* Mont., *Lejeunia Splitgerberiana* Mont., *Lejeunia flava* Sw., *Lejeunia phylloloba* Mont. et Nees.

2. C. Montagne, Quatrième Centurie, Ann. Sc. Nat., 1843, p. 23. — *Phragmicoma calcarata* Mont. (leg. Splitgerber) est noté. Plus tard, Montagne considère ce *Phragmicoma* comme semblable au *Lejeunia lunulata* (Web.) N. (*in* Cryptogamia Guyanensis, 1855).

3. C. Montagne, Sylloge generum specierumque Cryptogamarum, 1856. — Espèces citées: *Calypogeia Michelii* Mont., in Surinamo Batavorum (Hb Miquel); *Lejeunia surinamensis* M. ad folia in Surinamo (Splitgerber); *Lejeunia Splitgerberiana* M. in Surinam (Splitgerber); *Lejeunia Funckiana* N. ab E. Surinam (Funck).

4. Gottsche, Lindenberg, Nees ab Esenbeck, Synopsis hepaticarum, 1844. — Espèces citées du Surinam: *Lejeunia Funckiana* N. ab E.; *Lejeunia opaca* Gottsche (leg. Splitgerber); *Micropterygium vulgare* N. ab E., Lindb. et G.; *Lejeunia Sagraeana* Mont. var. *β minor* (leg. Splitgerber).

5. A. W. Evans, Hepaticae of Puerto Rico, Bull. Torr. Bot. Cl., 1908, 34, p. 553. — Une espèce citée du Surinam: *Mastigolejeunea auriculata* (Wils. et Hook.) Schiffn., Kegel leg.

6. A. W. Evans, Hepaticae of Puerto Rico, Bull. Torr. Bot. Cl., 1912, 39, p. 221. — Une espèce citée: *Diplasiolejeunea Rudolphiana* St., "Dutch Guiana, *Kegel*".

7. H. Reimers, Revision der Lebermoosgattung *Micropterygium*, *Hedwigia*, 1933, pp. 133-204. — Une variété citée du Surinam: *Micropterygium trachyphyllum* var. *guyanense*, notamment d'après une récolte de Weigelt.

8. F. M. Pagan, A preliminary list of the Hepaticae of Puerto Rico. The Bryologist, 1939, p. 42 et p. 78. — Espèces citées du Surinam: *Radula Kegelii* Gottsche, *Symbiezidium granulatum* (Nees) Trev.,

Symbiezidium barbiflorum (Lindenb. et G.) Evs. Ces deux dernières espèces sont, d'ailleurs, signalées à nouveau du Surinam par F. M. Pagan dans son "Catalogue of the Hepaticae of Guadeloupe" (The Bryologist, 1942, p. 106).

9. M. Fulford, Studies on American Hepaticae IV. — A revision of the genus *Symbiezidium*, Lloydia, 5, 1942, pp. 293–304. — Espèces citées d'après Stephani: *S. transversale* et *S. barbiflorum.*

10. M. Fulford, Studies on American Hepaticae — VI. *Ceratolejeunea*, Brittonia, 5, 1945, pp. 368–403. — Espèces citées du Surinam: *Ceratolejeunea cornuta* récolté à Paramaribo par Kegel (Cité par Lindenberg et Gottsche, 1851); *C. deciscens*, récolté par Focke, sans localité précise, cité par Sande Lacoste.

11. L. Clark et R. D. Svihla, The Bryologist, 1947, p. 383 et 1948, p. 239–242. — Espèces citées: *Frullania gymnotis; F. nodulosa* (Paramaribo, Hans; Lanjouw, 163).

Outre ces indications éparses, il faut citer la seule liste importante: Lindenberg et Gottsche, Plantae Kegelianae, Expositio Hepaticarum Surinamensium, *Linnaea*, 24, 1851, pp. 625–639. Les 42 espèces, variétés et formes récoltées par Kegel sont citées. Elles correspondent, en fait, à environ 39 espèces et variétés reconnues actuellement. Parmi ces espèces, 11 appartiennent aux genres *Plagiochila, Radula, Frullania*, *Dendroceros*, les autres à la famille des Lejeunéacées.

Ces données, fort intéressantes, restent cependant très insuffisantes et permettent seulement d'imaginer la richesse de la flore hépaticologique du Surinam.

Grâce à l'amabilité du Professeur Lanjouw et à l'aide précieuse de M. Florschütz, j'ai pu examiner quelques uns des nombreux spécimens d'Hépatiques contenus dans l'Herbier de l'Université d'Utrecht, et récoltés au Surinam. On trouvera, ci-dessous, la liste des espèces que j'ai nommées. Pour chacune, j'ai indiqué la distribution géographique actuellement connue, afin d'aider les botanistes qui s'intéressent au Surinam à mettre en évidence les relations floristiques entre ce pays et les contrées voisines.

Souvent, dans la collection étudiée, à un seul numéro de récolte correspondent plusieurs espèces; pour éviter de répéter autant de fois les détails concernant la localité et la station, il me semble préférable d'établir d'abord la liste des numéros de chaque collecteur avec les détails portés sur les étiquettes. Il suffira de noter ensuite, pour chaque espèce, le nom abrégé du collecteur et le numéro de la récolte.

Liste des spécimens récoltés

Bureau v. h. boswezen (B.W.), *6676 b* et *6676 c:* Hab. Bosreservaat Brownsberg. Epiphyllous on *Nectandra surinamensis* Mez., 28.X.1924.

J. et P. A. Florschütz. – *314:* Tosso-mountain between Tosso-creek and Sara-creek, virgin-forest; on decaying log; 18.XI.1950. — *687:* Near Zanderij, dark, marshy forest; on decaying trunk; 19.XII.1950. — *1489:* Ebba-mountain (Ebba-top), N. slope; open forest; epiphyllous; 15.II.1951. — *1518:* Base of Ebba-mountain

(Ebba-top), near camp; epiphyllous on small tree; 16.II.1951. — *1795:* Near km 121 (railroad); virgin forest on diabase-ridges; on twig of small tree; 17.III.1951. — *1797:* Near km 121 (railroad); virgin forest on diabase-ridges; on decaying wood; 17.III.1951. — *1808:* Near km 121 (railroad); virgin forest on diabase-ridges; on fallen tree; 17.III.1951. — *1815:* Near km 121 (railroad); virgin forest on diabase-ridges; on fallen tree; 17.III.1951.

D. C. Geijskes, *5 A:* Nassau-mountains, forest on plateau on decaying log; 30.IX.1952.

J. Lanjouw. — *746:* Coppename River, near Raleighfalls; epiphyllous; forest; 10.IX.1933. — *799:* Coppename River, near Raleighfalls; forest; on tree; 12.IX.1933.

J. Lanjouw et J. C. Lindeman. — *523:* Via secta ab Moengo tapoe ad Grote Zwiebelzwamp. Epiphyte from 0.5 3 m on trunk of tree; marshforest along Wane-creek; 28.IX.1948. — *525:* Epiphyte at about 1.5 m on trunk of tree. Via secta ab Moengo tapoe ad Grote Zwiebelzwamp; marshforest along Wane-creek; 28.IX.1948. — *1314:* Epiphyte on tree-root; Via secta ab via Wia-bank ad Grote Zwiebelzwamp; ridgeforest near km 12; 26.XI.1948. — *1945 A:* On dead tree; Tibiti savanne, Savanna-forest on third line; 15.I.1949. — *1946 A:* On dead trunk; Tibiti savanne, Savanna-forest on third line; 15.I.1949. — *2167:* Epiphyllous on *Tovonita;* in montibus qui dicuntur Nassau; in marshforest at km 1.3; 17.II.1949. — *2169:* Epiphyllous on *Oxandra asbecki;* in montibus qui dicuntur Nassau, in marshforest at km 1.4; 17.II.1949. — *2205:* Epiphyllous on *Poraqueiba guianensis;* in montibus qui dicuntur Nassau, in rainforest at km 1.8; 18.II.1949.— *2207:* Epiphyllous on *Pouteria gonggrijpii;* in montibus qui dicuntur Nassau; in rainforest at km 1.9; 18.II.1949. — *2230:* On decaying log; in montibus qui dicuntur Nassau; in rainforest, on slope at km 2.7; 21.II.1949. — *2399:* On trunk of small tree; in montibus qui dicuntur Nassau; in mountainsavanna-forest, at km 5.9, alt. 550 m; 1.III.1949. — *2453:* On dead log; in montibus qui dicuntur Nassau; in gully along small creek, km 6.8; 2.III.1949. — *2677:* On dead tree across creeklet; in montibus qui dicuntur Nassau, in gully near km 7; 14.III.1949. — *2832 A:* On dead log; capsule black on white seta; in montibus qui dicuntur Nassau; in rainforest, on slope, above km 10.5; alt. 450 m; 18.III.1949. — *Sans numéro:* Flora surinamensis, Expeditio Scientiae Naturalis 1948–1949; locality unknown.

J. C. Lindeman. — *3697:* On twigs of *Cheiloclinium cognatum;* Jodensavanne-Mapane kreek area (Suriname R.); in rainforest, in line 2; 26.III.1953. — *3923:* On base of *Humiria floribunda;* Jodensavanne-Mapane area (Suriname R.), in Savanna-forest, in line 2, p. 19; 12.V.1953. — *3933:* On base of tree; Jodensavanne-Mapane kreek area (Suriname R.); Savanna-wood fringing savanna, in line 2, p. 19; 14.V.1953. — *3935:* On base of tree; Jodensavanne-Mapane kreek area (Suriname R.); Savanna-wood fringing savanna, in line 2, p. 19; 14.V.1953. — *3937:* On base of tree; savanna wood fringing savanna, in line 2, p. 19; Jodensavanne-Mapane kreek area (Suriname R.); 14.V.1953. — *3938:* On base of tree; Jodensavanne-Mapane

kreek area (Suriname R.); savanna-wood fringing savanna, in line 2; p. 19; 14.V.1953. — *5997:* On decaying log; Rikanau prope Moengo; rainforest on Bauxite-hill; 29.V.1954. — *6011:* on base of shrub; Rikanau prope Moengo, in marshy shrub-savanna, in valley of Rikanau-creek. — *6012:* On base of shrub: Rikanau prope Moengo; in marshy shrub-savanna, in valley of Rikanau-creek; 2.VI.1954. — *6013:* On base of shrub; Rikanau prope Moengo; in marshy shrub-savanna, in valley of Rikanau-creek; 2.VI.1954. — *6015:* On base of shrub; Rikanau prope Moengo; in marshy shrub-savanna, in valley of Rikanau-creek; 2.VI.1954. — *6018:* On base of shrub; Rikanau prope Moengo, in marshy shrub-savanna, in valley of Rikanau-creek. — *7079:* On dead trunk; in secundary wood behind base camp at foot of Nassau-mountains, Marowijne River; 10.I.1955.

LEG. UNKNOWN, locality unknown, Suriname, epiphyllous hepatics, date?

LISTE DES ESPCÈCES RÉCOLTÉES

Lophocolea martiana Nees: Geijskes 5A; Lanjouw et Lindeman 2832A. Distribution: Amérique tropicale jusqu'en Floride. Semble nouveau pour le Surinam.

Bazzania acuminata (Lindenb. et G.) Trev.: Lanjouw et Lindeman 2453. Distribution: Mexique, Vénézuela. Nouveau pour le Surinam.

Bazzania Breuteliana (Lindenb. et G.) Trev.: Lanjouw et Lindeman 2399. Distribution: Cuba, Dominique, Guadeloupe, Jamaïque, Martinique, Porto Rico, St Kitts, Mexique, Costa Rica, Bolivie, Brésil, Colombie, Panama, Equateur, Pérou, Guyane anglaise. Nouveau pour le Surinam.

Bazzania cf *Liebmanniana* (L. et G.) Trev.: Florschütz 1808. Distribution: Mexique, Guatémala. Nouveau pour le Surinam.

Bazzania longa (Nees) Trev.: Lanjouw et Lindeman 2453. Distribution: Dominique, Cuba, Guadeloupe, Jamaïque, Martinique, Porto Rico, St Kitts, Trinidad. Nouveau pour le Surinam.

Bazzania longistipula (Lindenb.) Trev.: Lindeman 3933; Lanjouw et Lindeman 523. Distribution: Trinidad, St Vincent, Dominique, Guadeloupe, Porto-Rico, Saint-Domingue, Jamaïque, Colombie, Equateur, Pérou, Bolivie, Brésil. Nouveau pour le Surinam.

Bazzania platystipula Fulf.: Lindeman 6011, 6012, 6013. Distribution: Jamaïque, Porto Rico, Guadeloupe. Nouveau pour le Surinam.

Bazzania teretiuscula (L. et G.) Trev.: Lanjouw et Lindeman 523; Lindeman 3923. Distribution: Mexique, Costa Rica, Colombie, Equateur, Pérou, Bolivie, Brésil. Nouveau pour le Surinam.

Micropterygium trachyphyllum var. *guyanense* Reim.: Geijskes 5A; Florschütz: 314, 687, 1797, 1815; Lindeman: 3935, 5997, 6015, 6018, 7079; Lanjouw et Lindeman: 1314, 1945 A, 1946 A, 2230, 2832 A. Formant toujours de belles plaques compactes. Distribution: Barbade, Trinidad, Guyane française, Surinam, Vénézuela, Pérou.

Ceratolejeunea deciscens (L. et L.) St.: Lanjouw et Lindeman 523. Distribution: Guyane anglaise, Surinam, Brésil.

Ceratolejeunea maritima (Spr.) St.: Lanjouw 799; Lanjouw et Lindeman: 523, 2169, 2205, 2207, 2399, 2453, 2677; Lindeman 6015. Distribution: Trinidad, St Vincent, Ste Lucie, Martinique, Dominique, Guadeloupe, Barbade, Porto Rico, Jamaïque, Honduras, Costa Rica, Panama, Colombie, Equateur, Galapagos, Brésil, Guyane anglaise. Nouveau pour le Surinam.

Ceratolejeunea megalophysa (Spr.) St.: Lanjouw et Lindeman 2169 et, probablement, 2207. Distribution: Trinidad, Honduras anglais, Vénézuela, Brésil, Guyane anglaise. Nouveau pour le Surinam.

Ceratolejeunea plumula (Spr.) St.: leg. Unknown, sans n⁰ et sans date. Distribution: Trinidad, Martinique, Guadeloupe, Pérou, Brésil. Nouveau pour le Surinam.

Cheilolejeunea decidua (Spr.) Evs.: Lanjouw 799. Distribution: Floride, Antilles (Cuba; Porto Rico), Honduras, Panama, Brésil, Guyane. Nouveau pour le Surinam.

Colura Greig-Smithii S. J. - A.: Florschütz 1518; Lanjouw 746; Lanjouw et Lindeman: 2169, 2205. Distribution: Trinidad. Nouveau pour le Surinam.

Colura tortifolia (Mont.) St.: B. v. h. B. 6676 b; Florschütz 1518; Lanjouw et Lindeman 2205; Leg. Unknown, sans n⁰, sans date. Distribution: Trinidad, Martinique, Guadeloupe, Cuba, Equateur, Rio Negro, Guyane française, Guyane britannique, Surinam.

Crossotolejeunea crenata (Mont. et Nees) St.: Florschütz: 314,687,1797; Lanjouw et Lindeman: 1314, 2832 A. Le spécimen 2832 A, dont la détermination ne me semble pas douteuse (il y a des périanthes), présente, sur ses feuilles, 2 ou 3 ocelles basales et des ocelles éparses pleines d'une substance huileuse dorée. Ce détail n'est signalé dans aucune description de l'espèce. Distribution: Guadeloupe, Trinidad, Guyane, Surinam.

Cyclolejeunea chitonia (Tayl.) Evs.: Leg. Unknown, sans no et sans date. Distribution: St Vincent, Martinique, Guadeloupe, Porto Rico, Jamaïque, Vénézuela, Guyane anglaise. Nouveau pour le Surinam.

Cyclolejeunea convexistipa (Lehm. et Lindenb.) Evs.: Lanjouw et Lindeman 2169, 2205, 2207; Leg. Unknown. Distribution: très largement distribué en Amérique tropicale.

Cyclolejeunea peruviana (L. et L.) St.: Florschütz 1518; Lanjouw et Lindeman: 2167, 2205; leg. Unknown. Distribution: Martinique, Honduras, Costa Rica, Colombie, Pérou, Guyane française. Nouveau pour le Surinam.

Diplasiolejeunea brachyclada Evs.: Lanjouw et Lindeman 2169. Distribution: Jamaïque, Porto Rico, Guadeloupe. Nouveau pour le Surinam.

Diplasiolejeunea galloana S. J. - A.: Florschütz 1489; Lanjouw 746; Lanjouw et Lindeman: 2167, 2169, 2205; Leg. Unknown. Distribution: Guadeloupe, Guyane française, Surinam.

Diplasiolejeunea pellucida (Meissn.) Schiffn.: Lanjouw et Lindeman: 2169, 2205; Leg. Unknown. Distribution: Indo-Malaisie, Nouvelle Calédonie, Amérique tropicale. Espèce assez commune aux Antilles, en Amérique centrale et méridionale, par exemple: St Vincent, Martinique, Dominique, Guadeloupe, Porto Rico, Cuba, Jamaïque, Honduras, Costa Rica, Panama, Colombie, Pérou, Brésil, Guyane française. Semble nouveau pour le Surinam.

Drepanolejeunea cf araucariae St.: Lanjouw et Lindeman 2207. Distribution: Porto Rico, Brésil. Serait nouveau pour le Surinam.

Drepanolejeunea bispinulosa Evs.: Florschütz 1489; Lanjouw et Lindeman: 2169, 2207; Lindeman: 3937, 3938; leg. Unknown. Distribution: Guadeloupe, Porto Rico, Costa Rica. Nouveau pour le Surinam.

Drepanolejeunea inchoata (Meissn.) Schiffn.: Florschütz 1489; leg. Unknown. Distribution: Semble assez fréquent en Amérique tropicale et subtropicale, notamment Martinique, Guadeloupe, Porto Rico, Costa Rica, Colombie, Pérou. Nouveau pour le Surinam.

Euosmolejeunea trifaria (R. Bl. N.) St.: Lindeman 3937. Distribution: régions tropicales.

Leptocolea scabriflora (G.) Evs.: Florschütz 1518; Lanjouw et Lindeman: 2167, 2169, 2205, 2207; leg. Unknown. Distribution: Trinidad, Martinique, Guadeloupe, Porto Rico, Cuba, Jamaïque, Pérou, Brésil, Guyane. Nouveau pour le Surinam.

Leptolejeunea elliptica (L. et L.) Schiffn.: B. v. h. B. 6676 b; Lanjouw 746; Lanjouw et Lindeman: 2167, 2169, 2205. Distribution: régions tropicales d'Amérique, Asie, Iles du Pacifique. En Amérique, connu de la Floride jusqu'au Pérou.

Leptolejeunea stenophylla (Lind. et G.) Schiffn.: leg. Unknown. Distribution: Guadeloupe, Porto Rico, Cuba, Mexique, Honduras, Bolivie, Brésil, Surinam.

Lopholejeunea Howei Evs.: Lindeman 3937. Distribution: Porto Rico, Jamaïque. Nouveau pour le Surinam.

Microlejeunea bullata (Tayl.) Evs.: Lanjouw et Lindeman 2677. Distribution: Caroline du S, Floride, Antilles, Costa Rica, Equateur, Pérou, Brésil. Nouveau pour le Surinam.

Odontolejeunea lunulata (Web.) Schiffn.: Lanjouw et Lindeman: 1945 A, 2169, 2205; leg. Unknown. Distribution: largement distribué en Amérique tropicale; Afrique.

Pycnolejeunea macroloba (Mont.) Schiffn.: Lanjouw et Lindeman 2205; Lindeman 3937. Distribution: Costa Rica, Brésil, Guyane française. Nouveau pour le Surinam.

Pycnolejeunea decurviloba St.: Lanjouw et Lindeman 2453. Distribution: Trinidad, Equateur, Colombie. Nouveau pour le Surinam.

Rectolejeunea flagelliformis Evs.: Lanjouw et Lindeman 2169. Distribution: Porto Rico, Cuba, Honduras. Nouveau pour le Surinam.

Stictolejeunea squamata (Willd.) Schiffn.: Florschütz 1795; Lanjouw et Lindeman, sans numéro; Lindeman 3697. Distribution: St Vincent, Martinique, Dominique, Guadeloupe, Porto Rico, Haïti, Cuba, Jamaique, Honduras, Costa Rica, Panama, Brésil, Surinam.

Symbiezidium barbiflorum (L. et G.) Evs.: Florschütz 1518; Lanjouw 746; Lanjouw et Lindeman 525, 2677. Remarque à propos du spécimen n⁰ 525: D'après M. FULFORD (*Lloydia*, 1942, p. 298), *S. barbiflorum* est autoïque. Le n⁰ 525, à amphigastres nettement décurrents comme chez *S. barbiflorum*, est dioïque. Un spécimen de l'Herbier du Muséum (Paris) récolté par le Gouverneur Rey en Guyane française, appartient également à cette espèce et est dioïque. On pourrait en conclure que, comme *S. subrotundum*, *S. barbiflorum* peut être autoïque ou dioïque. Distribution: Trinidad, Martinique, Guadeloupe, Porto Rico, Cuba, Jamaïque, Honduras, Costa Rica, Panama, Colombie, Pérou, Brésil, Guyane française, Surinam.

Thysananthus amazonicus (Spr.) St.: Lindeman 3937. Distribution: Trinidad, Colombie, Brésil, Guyane anglaise. Nouveau pour le Surinam.

Frullania gymnotis Nees et Mont.: Lanjouw 799. Distribution: Guadeloupe, Jamaïque, Costa Rica, Brésil, Guyane française, Guyane hollandaise.

Le faible nombre d'espèces citées dans cette note ne permet aucune conclusion sur l'affinité de la flore hépaticologique du Surinam. On peut cependant noter que ces 40 Hépatiques comprennent: 3 espèces largement distribuées dans les tropiques, 3 espèces d'Amérique tropicale gagnant la Floride, 5 espèces d'Amérique centrale et méridionale, 7 signalées seulement aux Antilles (et en Guyane française pour 2 d'entre elles), 22 connues des Antilles et d'Amérique centrale et méridionale.

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A PALAEONTOLOGICAL STUDY OF A LAYER OF CLAY BENEATH AN INDIGENOUS SETTLEMENT FROM THE ROMAN PERIOD ON THE OUDE RIJN NEAR HAZERSWOUDE

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(with the assistance of A. VAN DER WERFF and Dr. C. W. WAGNER)*)

(*received September 27th, 1957*)

Dr. H. Brunsting, curator of the National Museum of Antiquities in Leiden, enabled the present writer, in April 1951, to study a layer of clay beneath a mound dating from the Roman period, situated at Hazerswoude, about 700 ms south of the Oude Rijn (co-ordinates on the Topographical Map: 99.2 and 459.6; see map no. 1 and no. 2). Dr. Brunsting hopes to give further information on the archaeological investigations later on. We only want to mention the date of the oldest (Roman) findings as about 50 years A.D.

The palaeontological study was made in three places situated at some metres distance from each other. They will be indicated here as Haz. A, B and C. Of Haz. A and B the entire layer of clay was analysed, of Haz. C (situated between A and B), by way of trial, only a sample at 2.30 ms—O.D. (O.D. = N.A.P.). The strongly disturbed, entirely dug up clay with remainders of the settlement was not studied. The underlying 60 cms of the clay investigated could be sampled in profiles. About 30 cms of it originated from the layer raised by man. For the sampling of the clay below the ground water-level a Dachnowsky sampler was used. It was not possible to take out the humic clay deeper than 140 cms (3.10 ms—O.D.), since the sampler touched a hard layer of wood. Besides clay of the Rijn also two potsherds of the settlement from Roman times were examined for diatoms.

In the following explanation we will discuss first the analytical study, outlined in a table and a pollen diagram. After that follows a short survey of what was discussed.

The tough, heavy clay was highly humous at the bottom, which contained much wood and bark of *Alnus*. Higher up the humosity decreased, while the percentage of lime increased. Little alder branches were still found up to 2.40 ms—O.D. At this depth also some *Alnus* fruits, as well as two little branches of *Scorpidium scorpioides* with leaves were found.

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The s.c. Phytolitharien (Ehrenberg, 1866), silicified cells of the epidermis of *Gramineae* (Grob, 1896 and Brockmann, 1940), indicate growth of grasses.

Mr. van der Werff examined the samples of Haz. A and B, as well as Haz. C 2.30 ms—O.D. for diatoms. No far-reaching conclusions with a high degree of certainty can be drawn from these analyses, since the number of recognizable specimens was very small, and in the three lower samples even nihil. However, some samples contained a fair number of fragments. We may assume with a fair amount of certainty that the deposition of the highly weathered clay under the settlement took place in an environment influenced by the sea and therefore became brackish now and then, but after that became fresh again for some time. From the small number of marine diatoms (which are often more resistant than most species living in fresh and brackish water) one gets the impression that the marine inundations only had an incidental character. From the oligohalob species found here (see table) it appears that the refreshening process after such inundations, which presumably carried the marine diatoms found, must have been complete or practically complete. This refreshening process must have been rapid, because in the same sample (which for a diatom analysis needs not to be large—in our case about 25 mm^3) species living in brackish water as well as those living exclusively in fresh water were found (the allochthonous species are left out of consideration). Whether such a conclusion is also pedologically justified, still remains a point of discussion, since the extent to which homogenization (Hoeksema, 1953) of deposits formed just below the surface of the water is not known.

On the ground of the diatom analysis it is not possible to say with any certainty whether also the water from the river played a part of any importance in this refreshening. Only in two samples (Haz. B and C at 2.30 ms—O.D.), and that in one single specimen, were species found which are abundant in rivers, namely *Melosira italica* and *Meridion circulare*. Both diatoms, however, are not specifically fluvial, least so *Melosira italica*. They were found, both by Mr. van der Werff and the present writer, several times in young-holocene peat and gyttja in the dunes. A better indication for river influences is the presence of *Coscinodiscus rothii* var. *subsalsa* (Haz. A 2.55 and 2.42 ms—O.D.). According to Hustedt (1930) this diatom lives apart from other places in the saltish water of a river mouth. Mr. van der Werff found the said variety for instance in a recent sample from the Biesbos. However, it is also found in young-holocene marsh deposits (i.a. just beneath the upper peat in the Osdorp polder between Amsterdam and Haarlem).

As to the food content of the water, it could be said that presumably the water has not always been eutrophic. For some diatoms do not find their optimum in a eutrophic environment, namely *Pinnularia nobilis* (optimal in oligotrophic water), as well as *Pinnularia microstauron* var. *brébissonii*, *Melosira arenaria*, *Meridion circulare* and *Melosira italica* (optimal in an oligotrophic or mesotrophic environment).

At 2.50 ms—O.D. (Haz. B) a fragment of *Pediastrum boryanum* was found. This algae species is sometimes found rather abundantly in shallow waters, swamps, etc.

According to information received from Dr. VAN VOORTHUYSEN, in the samples studied by him (Haz. B) no foraminifera were present. The phenomenon that the same samples contained marine diatoms, but no foraminifera, was repeatedly recorded and needs further explanation.

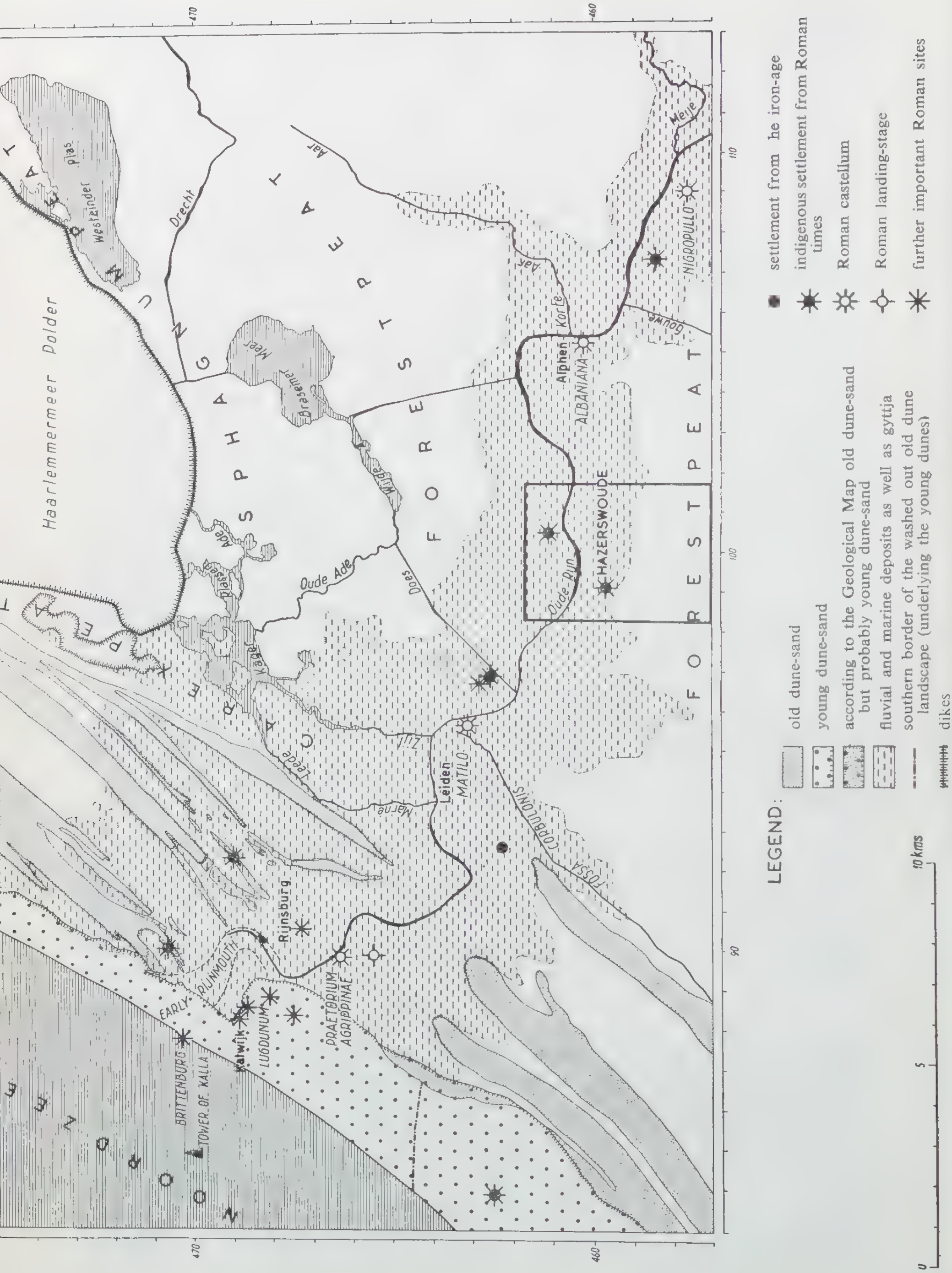
Needles of *Spongillidae* were found in every sample from Hazerswoude which was examined, in most cases even a great number of them. According to Mr. VAN DER WERFF they probably proceed from *Ephydatia fluviatilis* living both in stagnant and running fresh or brackish water.

Dr. WAGNER had the kindness to analyse the samples from Haz. B for ostracodes. They appeared to be present at depths of 2.40 and 2.30 ms—O.D. At 2.40 ms some intermediate stages of a *Candona*-species were found, probably *C. neglecta*. Judging from the analysis of the ostracodes, the clay from Haz. B 2.40 ms—O.D., according to Mr. WAGNER, was deposited in a fresh to very slightly saltish environment. The ostracodes found on 2.30 ms—O.D. (*Cytheromorpha fuscata*, *Candona neglecta*, *Darwinula stevensoni* and *Ilyocypris gibba*), according to information received from Mr. WAGNER, point to a fresh to slightly brackish environment. *Candona neglecta*, and also probably *Cytheromorpha fuscata* and *Ilyocypris gibba* are able to live both in stagnant and running water. *Darwinula stevensoni* appears to live frequently in ponds.

The baked potter's clay which was analysed contained relatively many marine diatoms, as well as a great number of needles of sponges, probably of *Ephydatia fluviatilis*. This clay was possibly deposited in a salt environment, in which refreshening took place. Its marine character suggests the potter's clay to have been dug not close to the settlement, but more seaward.

Both Haz. A and B were analysed palynologically. The clay proceeding from the mound was not analysed for pollen. Of the two pollen diagrams we shall only deal with that of Haz. B (Fig. 3). The other diagram does not differ in principle from it, and it will be discussed only incidentally.

The concentration of the pollen was on the whole sufficient; one or two preparations of 20 × 26 mms were enough for an analysis up to 150 tree pollen grains. Only the three lowest samples, which, as we have already stated, consisted for the greater part of wood, contained little or no pollen.


LEGEND:
settlement from he iron-age
indigenous settlement from Roman times
Roman castellum
Roman landing-stage
further important Roman sites
old dune-sand
young dune-sand
according to the Geological Map old dune-sand but probably young dune-sand
fluvial and marine deposits as well as gyttja
southern border of the washed out old dune landscape (underlying the young dunes)
dikes
0
5
10 kms
470
460
110
100
90
Haarlemmermeer Polder
Westeinder plas
Drecht
Aar
Meer
Brasemer
Wijde
Ade
Oude Ade
Does
Kager
Leede
Zijl
Marne
Leiden
MATILO
CORBULONIS FOSSA
Rijnsburg
EARLY RIJNMOUTH
Katwijk
LUGDUNUM
BRITTENBURG
TOWER OF KALLA
PRAETORIUM AGRIPPINAE
SPHAGNUM PEAT
FOREST PEAT
Alphen
ALBANIANA
Aak
Korte
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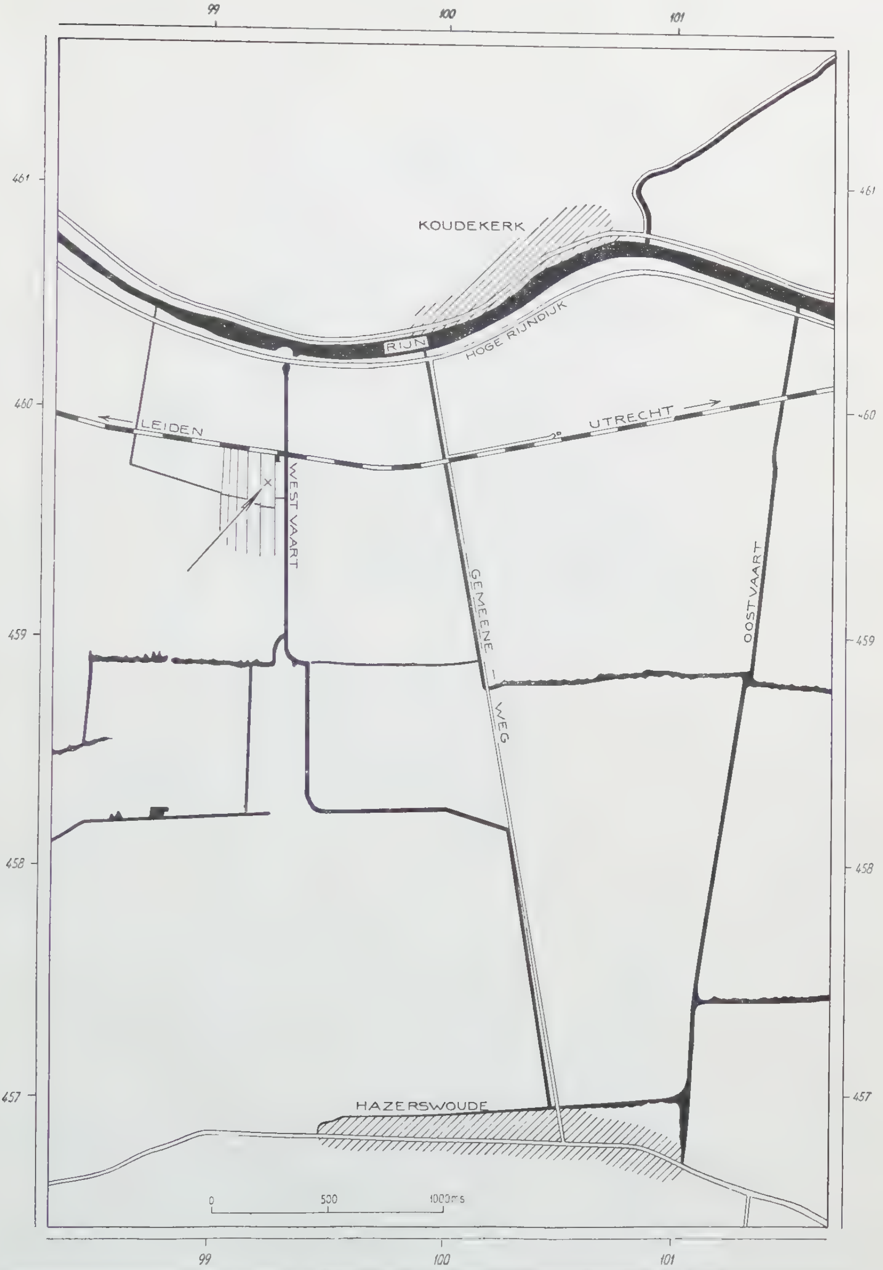
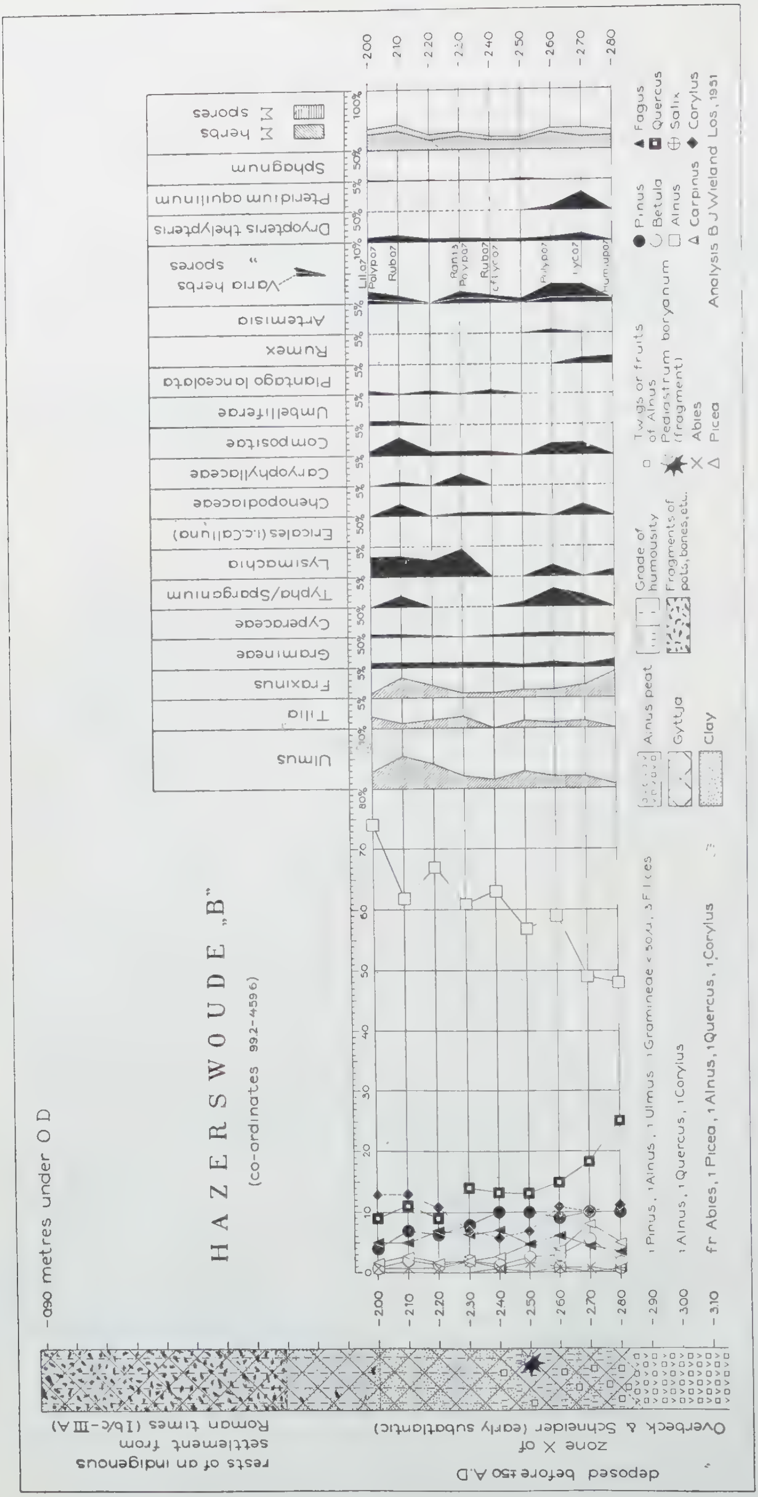
NIGROPULLO
HAZERSWOUDE
Oude Rijn



Map of foregoing page:

General geo-archaeological map of the mouth of the Oude Rijn with the most important findings from the iron age and from Roman times.

As for the geology the present writer used the Geological map (1:50.000), the peat map of Bennema (1949) and the soil map from the thesis of van der Meer (1952). The southern border of the washed out old dune landscape was indicated by the director of the N.V. Leidsche Duinwater Maatschappij, Dr. Ir. P. C. Lindenbergh. The archaeological data are derived from different sources. A more elaborate archaeological map with an explanation is in active preparation.



Abbreviations used:
Lil. = Liliaceae; Polyp. = Polypodium; Rub. = Rubiaceae; Ran. = Ranunculaceae; Lyc. = Lycopodium; Hum. lup. = Humulus lupulus

neritic or benthal	epontic	planktonic	oligotrophous	mesotrophous	eutrophous	oligohaline	euryhaline	stenohaline	chloring degree	m — O.D.	Hazerswoude A										B													C
											— 2.35	— 2.42	— 2.50	— 2.55	— 2.62	— 2.70	— 2.85	— 2.90	— 3.00	— 3.10	— 1.70	— 1.80	— 1.90	— 1.95	— 2.00	— 2.10	— 2.20	— 2.30	— 2.40	— 2.50	— 2.70	— 2.80	— 3.10	— 2.50 8)
										FLAGELLATAE, cysts; (A. van der Werff).															rr									
										DIATOMEAE; (A. van der Werff).																								
×		×			×			×	M	*Aulacodiscus argus* (Ehr.) A.S.				f													f		f					rr
×		×			×		×		M	*Opephora pacifica* (Grun.) Petit																		r						
×		×			×			×	M	*Podosira stelliger* (Bail.) Mann					f											r	rr	rr	f					rr
×		×			×			×	M	*Thalassiothrix* sp. (? *frauenfeldii* Grun.)																								rr
×		×			×			×	M	*Triceratium favus* Ehr.																r		r						
		×			×		×		MB	*Actinoptychus undulatus* (Bail.) Ralfs.																		r						
×		×			×		×		MB	*Diploneis bombus* Ehr.				f																				
		×			×		×		MB	*Hyalodiscus scoticus* (Kütz.) Grun.					rr	rr					rr				r			r	rr					
×		×			×		×		B	1) *Campylodiscus echeneis* Ehr.																								rr
		×			×		×		B	*Coscinodiscus rothii* (Ehr.) Grun. var. *subsalsa* (Juhl-Dannf.) Hust.		f		rr																				
×					×		×		BZ	*Navicula rostellata* Kütz.													rr											
	×	×		×	×		×		ZB	*Cocconeis placentula* Ehr.													rr					r						
		×		×	×		×		ZB	2) *Epithemia turgida* (Ehr.) Kütz.																		r	f					
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×		×		×	×		×		ZB	4) *Gyrosigma attenuatum* (Kütz.) Rab.															f									
		×	×	×		×			ZB	*Melosira italica* (Ehr.) Kütz.																		o						
		×	×	×		×			ZB	5) *Meridion circulare* (Grev.) Ag.																								rr
×		×		×	×		×		ZB	*Surirella ovata* Kütz.		rr																						
×	×	×		×	×		×		ZB	*Synedra ulna* (Nitzsch) Ehr.													rr											rr
×		×	×	×		×			Z	6) *Melosira arenaria* Moore; (B. J. Wieland Los)														rr										
×		×	×	×		×			Z	*Pinnularia microstauron* (Ehr.) Cl. var. *brébissonii* (Kütz.) Hust.											rr													
×		×	×	☐		×			Z	7) *Pinnularia* sp. (? *nobilis* Ehr.)																		r						
										CHLOROPHYCEAE.																								
		×		☐	×				ZB	*Pediastrum boryanum* (Turp.) Menegh.; (B. J. Wieland Los)																				f				
										BRYOPHYTA; (Prof. Dr. R. van der Wijk)																								
				×	(k) ×				Z	*Scorpidium scorpioides* (Hedw.) Limpr.																			•					
										ANGIOSPERMAE.																								
									MBZ	"Phytolitharien"; (A. van der Werff).																			r					
										rootlets of *Carex* sp.		•																						
									(M-B)Z	fruits of *Carex* (div. sp.)																								
									(ZB-Z)	*Alnus* sp., twigs.																			rr	r	+	cc	cc	
				☐	×	×			(ZB-Z)	*Alnus* sp. (? *glutinosa* Gaertn.), fruits																			+					
										FORAMINIFERA; (Dr. J. H. van Voorthuysen)																								
	×			×	×		×		B-ZB	*SPONGILLIDAE*, needles, probably of *Ephydatia fluviatilis* L; (A. van der Werff).	r	r	r	r	r	r	+	+	r	r	+	r	r	+	+	+	+	+	r	r	r	r	r	c
										OSTRACODA; (Dr. C. W. Wagner).																								
×						×	×		ZB	*Cytheromorpha fuscata* (B.)																		a)						
×						×	☐		ZB	*Candona neglecta* Sars																		b)						
									(ZB)	*Candona* cf. *neglecta* Sars																			c)					
×						×			ZB	*Darwinula stevensoni* B. et R.																		d)						
×						×			ZB	*Ilyocypris gibba* (Ramdohr)																		e)						
										MOLLUSCA; (Dr. C. O. van Regteren Altena)																								
										undeterminable, thin-walled fragments.																								f

neritic or benthal	epontic	planktonic	oligotrophous	mesotrophous	eutrophous	oligohaline	euryhaline	stenohaline	chloring degree	Analyses on fragments of "Fries-Batavian" pottery; (A. van der Werff)	fragm. no 1	fragm. no 2
×		×								*FLAGELLATAE*, cysts	r	
										DIATOMEAE		
×		×			×			×	M	*Aulacodiscus argus* (Ehr.) A.S.	r	r
×		×			×			×	M	*Melosira sulcata* (Ehr.) Kütz.		r
×		×			×			×	M	*Melosira westii* W. Sm.	r	
×		×			×			×	M	*Podosira stelliger* (Bail.) Mann	r	r
×		×			×			×	M	*Triceratium favus* Ehr.	r	r
	×		×	☐					Z	9) *?Melosira roeseana* Rabh.	r	
										Diploneis sp.	f	
	×			×	×		×		ZB	*SPONGILLIDAE*, needles, probably of *Ephydatia fluviatilis* L.	c	c

a) 1 ad. ♀, some juv. b) 6 ad. ♀, 1 ad. ♂?, 20 juv. c) some juv. d) 2 ad. e) 1 ad., 1 juv.

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1) *Campylodiscus echeneis* Ehr. According to Cleve-Euler (1952) also found in almost fresh water, according to Mr. van der Werff optimal in saltish water. A typical representative of sandy coastal districts, (muddy) sand-banks, etc., in our case probably allochthonous.

2) *Epithemia turgida* (Ehr.) Kütz. According to Cleve-Euler (1952) very frequent in slightly brackish water.

3) *Epithemia zebra* (Ehr.) Kütz. According to Cleve-Euler (1952) very frequent in fresh water, seldom in brackish water. Mr. van der Werff informed me that, with respect to the degree of salinity, he has found little or no difference between *E. turgida* and *E. zebra*.

4) *Gyrosigma attenuatum* (Kütz.) Rab. According to Cleve-Euler (1952) typical of its "clear water flora". However, Mr. van der Werff found this diatom also at Abcoude, where the water is in general not clear. *G. attenuatum*, according to Cleve-Euler, is minerotrophic.

5) *Meridion circulare* (Grev.) Agardh. According to Cleve-Euler (1953) not present in big lakes and calciphilous; according to Mr. van der Werff and the present writer the latter is not obligatory.

6) *Melosira arenaria* Moore. According to Hustedt (1930) frequently found on the shores of European lakes, particularly on flat, sandy shores, sometimes also in rivers and ditches. Cleve-Euler (1952) considers this species typical of clear water. She found it more frequently as a fossil than as a recent species. In our country Mr. van der Werff has not yet found living species of *Melosira arenaria*. He did find it in a sandy deposition of a pond of the former country-seat [illegible] (XVIIth and XVIIIth century) at Velsen (a study by the present writer in 1954).

7) *Pinnularia nobilis* Ehr. According to information received from Mr. van der Werff sometimes also in a mesotrophic environment, e.g. in the Oosterwijk ponds. According to Cleve-Euler (1953) in lakes and swamps. In this case no trophic-indication was given.

8) analysis B. J. Wieland Los.

9) *Melosira roeseana* Rabh. Aerophilous (Cleve-Euler, 1951; Weckering, 1953), cold stenothermic (Cleve-Euler, 1951) fresh water diatom, which is especially found in mosses and on inundated stones (Hustedt, 1930), and authors mentioned before, e.g. humid rocks and mosses along the banks of brooks, naturally in the mountains in particular, less in the low-lying plain (Hustedt, 1930).

Abbreviations used (chloring degree mg/l)

M = 18.000; MB = 18.000–10.000; B = 5.000–1.000; BZ = 1.000–500;
ZB = 500–100; Z = 100

• = present; + = common; c = very common; cc = abundantly; rr = extremely rare; r = rare; f, ff = fragment(s); o = cyst; juv. = juvenal; ad. = adult; × = regularly found in a specific environment; ☐ = occasionally found in a specific environment ;(k) = facultative calciphilous.

The pollen had generally been well preserved. Only at the dephts of 2.50 and 2.30 ms—O.D. the material was slightly affected.

The percentages of *Fagus* are characteristic of the beginning of the subatlantic of the central and northern parts of the Netherlands. The low *Carpinus* values point to period X of OVERBECK and SCHNEIDER (cf. VAN ZEIST, 1955), with which in general the subatlantic is considered to begin. Further it is notable that higher up *Alnus*, which dominates in our diagram, increases at the cost of *Quercus*. The percentages of *Ulmus* correspond more or less with those which are found in general in subboreal and subatlantic spectrums in our country, those of *Tilia* are somewhat higher. No conclusion about the presence of this tree in the area around the mouth of the Oude Rijn—WATERBOLK (1954) even presumes that *Tilia* disappeared from our natural vegetation in the course of the subboreal—can be drawn from it, because we have to consider the appearance of secondary pollen. An indication of it are the relatively high percentages of pollen of *Picea* and *Abies*, trees which presumably are not indigenous. In our case the *Picea*- and *Abies* pollen will most likely not have been carried by air, but by water. A similar phenomenon was found by FLORSCHÜTZ and JONKER (1939) in postboreal (river)clay near Wijk bij Duurstede. In this case there were moreover high percentages of *Pinus*, whilst the *Fagus* curve was irregular. In our case neither is the case. FLORSCHÜTZ and JONKER think it probable that part of the pollen contained in the clay analysed by them was brought down from the woods of the upper Rijn. They drew the attention to the fact that *Picea*, *Abies* and *Fagus* strongly extended there during the atlantic and subboreal. Besides this hypothesis of FLORSCHÜTZ and JONKER there is still one of POLAK (1936*a* and *b*), namely that deposits rich in *Picea*- and *Abies* pollen are washed by a river or by the sea and that the pollen liberated by it is deposited on other places. This latter theory was suggested by FLORSCHÜTZ (1953), who found *Picea* pollen in a deposit from the aeneolithic period at Hekelingen (situated about 12 kms southwest of Rotterdam). Not only from a detailed survey made by BENNEMA (1953), but also from a diatom analysis by the present writer, it has appeared that besides marine influences, also fluvial influences (estuary) have played a part in this place, so that it is possible that just as in Wijk bij Duurstede the *Picea* pollen was brought down by the Oude Rijn. To me this seems the most plausible explanation for our diagram. More seaward, however, namely near the castellum of Valkenburg (*Praetorium Agrippinae*, see map no. 1), it was the sea, according to VAN ZEIST (1953) which brought secondary pollen (also of *Pinus*).

The percentages of non-arboreal-pollen and spores are low, which points to a woody environment. From the low *Chenopodiaceae* values it appears that also in the Hazerswoude area marine influences (which, as we have seen when speaking of the diatom analyses, must have occurred on the spot in small numbers) were not important. When judging the *Chenopodiaceae* curve, we must bear in mind that a number of *Chenopodiaceae* are not halophilous or need not be represented as such.

Lysimachia was common. The *Lysimachia* species grow in an mesotrophic or eutrophic environment, in humid soil or in a moor and are not anemophilous. The relatively rather high percentages suggest that *Lysimachia* lived on the spot or very near to it. Of *Typha* which will no doubt have been present in this wet environment pollen was found several times. *Humulus lupulus* fits well in an alder wood. As to *Polypodium*, one would think rather of a place with oaks. The spores of *Pteridium aquilinum* will probably have proceeded from plants growing in the dunes.

Plantago lanceolata was found three times in the two diagrams, which means 2 $^0/_{00}$ on a average. In early subatlantic spectrums of the upper peat near Zaandam I found it more frequently (up to 3 %). Compared with Kennemerland the area of the Oude Rijn was therefore thinly populated, or rather cattle-breeding was of little significance.

Summarizing the foregoing, we may say that the subatlantic humous clay-gyttja analysed by us (dating before the first decades of the first century) was deposited in a wooded area, namely in a shallow, overgrown pool, which contained on the whole eutrophic water, but which presumably was sometimes a little less nutritious. The water was often fresh, though sometimes mesohalinic to polyhalinic; the latter probably only after high tides. The complete change into fresh water suggests that there was a regular mixing with fresh water. The place studied may have been a quiet spot near the mouth of a river in the sense of Vink (1926), i.e. a broad stream, now not running at all, now running slowly, connected with the middle course of a river and receiving nutrition salts from it, and carrying silt only at high tide.

The water level must have gradually risen. Owing to the depositing process however, the depth of the water did not increase considerably. A raise of the water level around Hazerswoude is the most plausible explanation of the phenomenon established by us by means of the pollen analysis that the oak wood was replaced by an alder wood.

During the silting-up of the area around Hazerswoude it was insuitable for habitation. So far we know in the entire area of the Oude Rijn only one settlement from the (pre-Roman) iron age. In the Roman period, however, this area was relatively densily populated (see map). This does not only apply to the levee soils, where we may expect older settlements as well, but also to the clay area. Before man settled here, however, he first raised the level of the earth. Since the inhabitants must have had arable land and meadows, too, we can safely assume that regular human habitation was only possible after a fall of the water level.

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ON THE ARILLOIDS OF NEPHELIUM, EUPHORIA, LITCHI AND AESCULUS, AND THE SEEDS OF SAPINDACEAE IN GENERAL

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A. Introduction

The seeds of the *Sapindaceae* show some remarkable features. One of them is the "*Wurzeltasche*" or radicular pocket, separated from the main part of the seed by a "deep fold of the testa".

Another noteworthy feature is the pluriformity of the fleshy parts round or near the seed. The fleshy part may belong either to the seed itself or to the pericarp. Radlkofer, the well-known specialist on the *Sapindaceae*, originally used the term aril for all these fleshy parts, which means that he used it in an ecological sense. In his study on the "aril" of *Sapindaceae* (1878) he proposed to use the terms: *a*) arillo epispermatico, *b*) a. esostomatico, *c*) a. ombelicale-esostomatico, *d*) a. ombelicalo and *e*) a. endocarpico, for those, morphologically heterogeneous, structures. In this paper these structures will be designated as follows, *a*) sarcotesta (fleshy testa), *b*) micropylar arillode, *c*) micropylar-chalazal arillode (*b* and *c* are fleshy parts of the testa restricted to a definite area), *d*) true aril, and *e*) endocarp pulpa.

In later years Radlkofer (1895) gave a short review of the fruit forms occurring in this family, in which he designated the fleshy layers with the convential names. He seemed to think that the phylogenetic sequence of the structures *a*, *b*, *c*, *d* was *d-c-b-a*, which means that he regarded the sarcotesta, of e.g. *Talisia*, as the final stage. On the seeds of *Xerospermum*, which apparently are provided with a sarcotesta, he said that they possessed a fleshy aril that was completely fused with the seedcoat. The sarcotesta of the genera *Synima* and *Lychnodiscus* was presumably interpreted by him in the same way.

In his large monograph of 1933/1934 he gave no general review, but inserted many remarks on the arilloid structures found in individual species. In this work he criticized at several points the current fashion to describe every fleshy part that does not belong to the outer pericarp as an aril.

In later years the morphological investigation of the various kinds of testa found in the Sapindaceae has made but little progress.

Mauritzon (1936*a*) figured the ovules of some species of *Sapindus*, *Xanthoceras*, *Nephelium*, *Koelreuteria*, *Dodonaea*, *Diplopeltis* and *Cardio-*

spermum. He described cases in which the thick nucellus was, during anthesis, gradually resorbed, of an unusually broad insertion of the ovule, of the campylotropous incurvation of the ovule during its later development, and of the outer integument's tendency to swell in the micropylar region. He paid, however, little attention to the vascular supply of the ovule and to the development of the testa.

CORNER (1953) paid some attention to the family when he was in search for support for his "Durian Theory", which regards the arillate seed as primitive.

The sarcotesta of the *Melicocceae* was by him too considered as "a modification of the aril: in some obscure manner the aril becomes adnate to the testa in many allied *Nephelieae*". In some of them (*Nephelium*, *Cubilia*, *Pometia*) and also in *Blighia*, *Paullinia* and *Schleichera* he considered the fleshy part on the outside of the seed as an aril.

In 1955 I published a study on the typological derivation, or, possibly, the evolution, of fleshy parts in the fruits of the *Angiosperms*. I tried to prove the primitiveness of the fleshy seedcoat, or sarcotesta (phase *a*), and adduced arguments in support of Corner's idea that the current notion of the primitive seed as a small, hard, dry and dormant organ is to be abandoned. I criticized, however, his undiscriminate use of the term aril, and I demonstrated that in contrast to Corner's opinion, most so-called arils are arillodes and that even parts that are usually designated as a "true funicular aril" are in many instances derivative products, viz. specialized and individualized outgrowths of the integument. I already found support for this view in some *Sapindaceae*, where many "arils" are in reality arillodes, arising from the integument.¹)

I have already elaborated my view on the primitive character of the sarcotesta for the *Leguminosae* (1956), and wish to do now the same for the *Sapindaceae*, in order to show that, here too, the same above already mentioned developmental range *a-e* is present.

First of all, however, I wish to make some general remarks.

The discussion on the nature of the aril is, as I perceived a short time ago, the revival of a controversy which arose a century earlier (cf. the review given by PFEIFFER (1891)). BAILLON (1875) took, in a study not reviewed by PFEIFFER, the same stand as I do now. He regarded an "*arille généralisée*" (our sarcotesta) as the starting point from which various arilloid structures arose by reduction; the latter were his "*arilles localisées*". He demonstrated this in *Myristica*, some *Zingiberaceae*, *Euphorbiaceae* and *Rhizophoraceae*. MAURITZON (1936*b*) studied "arils" from some of the families which according to Corner are provided with arillate seeds. In *Careya arborea* (*Lecythidaceae*), *Strelitzia*, *Costus*, *Globba* and *Alpinia* (*Scitamineae*) these "arils" proved

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¹) I wish to make here a correction in the table given in my study of 1955. Among the *Palmae* the *Lepidocaryeae* (*Zalacca*, *Metroxylon*, *Daemonorops*, *Plectocomiopsis*, *Calamus*, etc) are not provided with a pulpy endocarp, as stated there with a question mark. According to BECCARI (1918) the fleshy mass around the seed is part of the latter.

to be arillodes developed from the integument parts indicated in Fig. 1 by *a* and *c*.

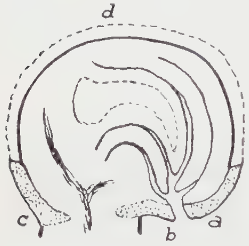

Fig. 1. Schematical median section of a sapindaceous ovule with the regions of the outer integument which may contribute to the development of arillodes dotted. In a complete sarcotesta *d* too is fleshy.

Finally I have to discuss some definitions of terms used in this paper.

Pfeiffer (1891) defined the aril as an outgrowth of a part near the seed and attached only at its place of origin. Although this definition agrees in the main with my own conception, does not prevent us from regarding the aril as a secundary structure, and excludes the sarcotesta, it seems to me too wide, as it would include also Radlkofers "arillo endocarpico", the endocarp pulpa (found in some *Guioa* and *Pseudima* species).

Though Mauritzon (1936*b*, 1939) showed that arilloid structures may sometimes be developed before fertilization has taken place, I propose to define the aril more or less in the same way as Gaertner did of old, viz. as a secundary, usually postfloral outgrowth of the funicle and therefore entirely free from the seed. This definition is independant of whatever view we may hold with regard to the phylogenetical origin of the aril.

While maintaining the old term "arillode" for an outgrowth of the integument in the vicinity of the micropyle, I shall use the term "arilloid" for every kind of outgrowth on and near the seed that resembles the apparently entirely independent aril.

B. Observations

Cupania hirsuta Radlkofer (*Cupanieae*)

I could study the ovules of flowers in anthesis. They show a slightly curved nucellus, which in this species persists up to this period, but might nevertheless be described as anatropous.

There is no distinct funicle, and the ovule is inserted directly on a horizontal outgrowth, apparently of the central "axis". The outgrowth is widened transversely, and acts as a kind of secundary placenta. It projects past the place of insertion of the ovule, and forms underneath the micropyle a kind of obturator (Fig. 2).

The outgrowth of the placenta possesses a vascular supply consisting of several bundles. A large bundle enters the ovule; this is the raphal bundle. It does not branch into separate integumental bundles as is frequently seen in the family. The raphal region is more or less swollen.

As I did not have older stadia, I could not make out from what part the cupuliform aril, whose presence has been reported for the genus, arises.

I started with the description of the situation found in this species, as it seems to be a rather simple one, from which that which we will meet in other genera may be derived.

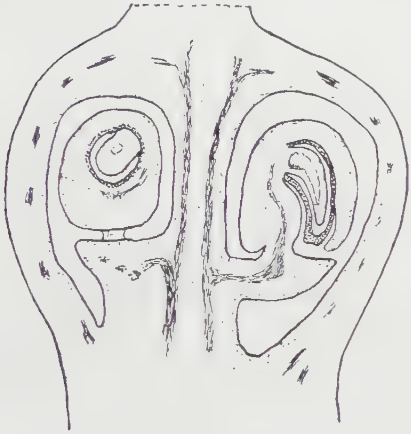

Fig. 2. *Cupania hirsuta.* Longitudinal section of ovary during anthesis. Left ovule cut obliquely, right one according to the plane of symmetry.

Nephelium lappaceum L. (Nephelieae)

Radlkofer (1933) says that the edible part of the fruit is an aril, adnate to the thin testa, and only free from the latter around the micropyle. He considers it as a far advanced stage in the developmental range mentioned in the introduction.

However, a study of the ontogeny of the seed shows that the fleshy layer is in reality the swollen outer integument (Fig. 3). The broadly

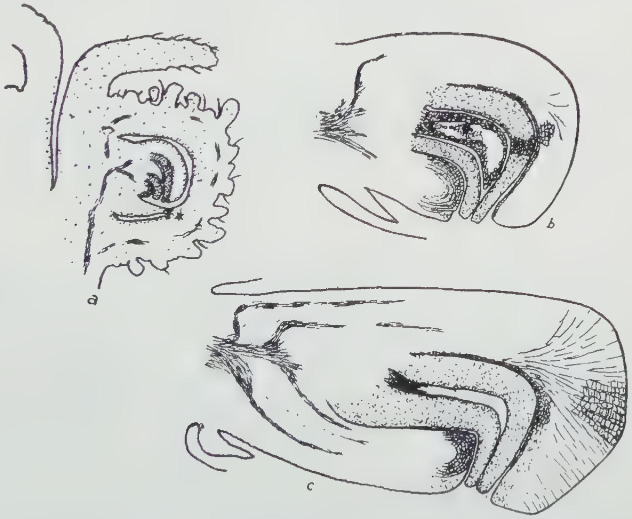

Fig. 3. *Nephelium lappaceum.* Longitudinal sections of ovarium and ovules, *a.* very young ovary, *b.* ovule at the time of fertilization, *c.* a long time after fertilization.

attached ovule grows out in a longitudinal direction, and the cells of the outer integument become very large. Near the tip they are arranged in rows that radiate fanwise. Sometimes these rows of cells end in the epidermis, which suggests an epidermal origin, but sometimes they end (or better start) subepidermally. The dry "inner testa" underneath it probably originates from the innermost layer of the outer integument and from the inner integument. The cells of these layers remain small. As the two integuments remain for the greater part firmly connected, it proves difficult to detach the pseudo-aril from the inner layers. When this has been done forcibly, the "seed" shows, of course, no true hilum.

When we study longitudinal sections of ovules during anthesis, the triangular outgrowth in the angle between ovule and pericarp might suggest a future aril. However, this outgrowth, which surrounds a large part of the base of the ovule, is not meristematic and does not develop further. It reminds one of the outgrowth of the placenta found in *Cupania*. In very young ovules (Fig. 3*a*) it looks like a transverse sept extending from the placenta to the ovary wall. The existence of a connection with the ovary wall, however, remains uncertain, as the supposed connecting cells near the asterisk in Fig. 3*a* are more or less free from each other and desintegrate entirely in a subsequent stage. This situation elucidates to some extent the one found in *Cupania*. There, however, the ovule proper still shows something like a real raphal bundle. It looks as if in *Nephelium* the basal part of the ovule is not just an unusually broad funicle, but that it includes placental tissue.

In transverse sections of fertilized ovules we have studied the vascularization. A very thick vascular column composed of radially arranged bundles, runs through the basal part. At a higher level it splits into two concentric rings of small bundles which enter into the outer integument. There is no median bundle, and it is therefore hardly possible to speak here of a raphe.

As the ovule grows out in a longitudinal direction only, the campylotropy of the ovule gradually disappears, and is no longer recognizable in the mature seed. Consequently there is no fold in the testa.

Paullinia (*Paullineae*)

In my earlier study (1955) I already pointed to the seed of the well-known *guarana*, *Paullinia cupana*, as of the utmost importance for the interpretation of the sapindaceaus arilloids.

The "aril" here is considered by RADLKOFER (1933) as an adnate arillodium, and by CORNER (1953) as an adnate aril.

I found that it is merely a partial sarcotesta, an arillode, the fleshy parts corresponding with those which in Fig. 1 are indicated with the letters *a*, *b* and *c*.

The following two facts seem to be decisive in this respect:

a) the micropyle is visible in the middle of the arillode, which would be impossible if an aril had grown over it, *b*) the so-called "aril" does not consist of a distinct tissue fused with that of the testa, but is to be regarded as a mere change in the texture of the testa itself (cf. *Cardiospermum*).

In *Paullinia boliviana* Radlk. the arillode shows an outgrowth at its rim. This envelops the rest of the seed for some distance, thus assuming a more aril-like aspect.

If the zone of the testa to which the arillode is attached becomes narrower the latter may at first sight be hardly distinguishable from a true aril arising from a funicle and remaining entirely free from the testa.

When a seed with a broadly attached arillode like that of *Paullinia* is detached, the hilum becomes visible. When subsequently the arillode is torn off, a much larger scar is left. We shall call this second scar the pseudo-hilum.

In the seeds of *Durio* and *Euonymus*, which also are provided with arillodes, we find the same large scar on the seed.

The seeds of *Aporrhiza*, with a half dry, half fleshy testa are similar to those of *Paullinia*.

Harpullia arborea (Blanco) Merr. (*Harpullieae*)

The almost mature seeds I could investigate, were dark brownish-green and bore the fleshy, orange outgrowth that is characteristic for the genus, and which generally has been described as an aril. Radlkofer (1933) calls this species exarillate, but in all the herbarium specimens seen by me the arillode was well recognizable, though strongly shrivelled.

It is easy to prove that it is an arillode of the *Paullinia*-type, not adnate to the testa, but part of it. Sections of an ovule shortly after fertilization (Fig. 4) show that the latter is provided with a funicle, and that the fleshy mass originates in a circular zone which surrounds the micropyle and the chalaza and belongs to the outer integument (part *a* in Fig. 1) and to the raphe region (part *c* in Fig. 1). In the other parts of the ovule the outer layers change at an early stage into ordinary, dry testa tissue. The epidermis of these dark parts extends for some distance over the arillode, and this too seems to prove that the arillode can not be regarded as an originally distinct part.

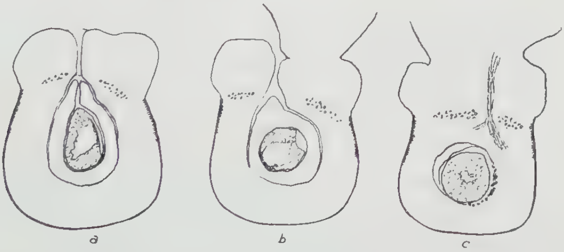

Fig. 4. *Harpullia arborea.* Three sections out of a series cut through an ovule shortly after fertilization.

Dark-coloured, sclerified or cutinized cells are seen at an early stage in the deeper layers of the arillode where they form the continuation of the dry parts of the testa, and serve as a protective shield underneath the arillode. When the arillode is removed, a pseudohilum is left.

A view of the mature arillode from above (Fig. 5*b*) and a section of it perpendicular to the micropylar canal (Fig. 5*c*) show that the region indicated in Fig. 1 by *b*, does not develop into arillode tissue. This part is covered by extensions of the tissue formed in the parts *a* and *c*. The groove between these two parts of the arillode persists even in the ripe seed. The micropylar canal in the upper part of the arillode is extremely narrow, and disappears in its lower part; it is not lined by special cells. On longitudinal sections (Fig. 5*a*) it can, therefore, not be detected. A non-sclerified spot in the partition layer indicates the place where the radicle will perforate the testa at germination.

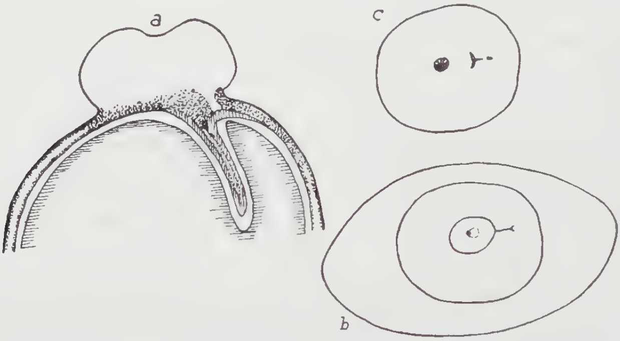

Fig. 5. *Harpullia arborea*. Arillode of mature seed. *a*. longitudinal section, almost median, with intrusion and embryo, *b*. surface view from above with arillode, hilum, suture and micropyle, *c*. cross section of upper part of arillode with bundle, suture and canal.

Cardiospermum halicacabum L. (*Paullineae*)

The seed is well-known for its white, heart-shaped mark. The latter is sometimes considered as a hilum, sometimes as a dry aril. RADLKOFER (1933) described it as a hilum.

In the heart-shaped mark we find the micropyle near the notch and the scar of the vascular bundle near the point.

We possess three studies dealing with the ontogeny of the seeds, viz. by GUÉRIN (1901), MAURITZON (1936*a*) and KADRY (1946). (The more general study on the sapindaceous testa promised by Guérin, has never appeared, as far as I know). The study by Mauritzon gives no details that might interest us here. The other two studies contradict each other in some respects. Guérin gave drawings which leave us in some doubt with regard to the exact origin of the arillode. He regarded it as an extra-layer over the testa.

Kadry interpreted his Fig. 15*a* as showing a micropylar beak, a massive mucilaginous tissue originating from the tip of the nucellus and from part of the inner integument. He contested the correctness of Guérin's opinion that this beak surrounds a micropylar canal. Guérin's Fig. 1, the structure generally found in the ovules of the family and my own sections through these ovules make it clear that this beak is nothing but the tip of the solid looking inner integument, and that the nucellus has been resorbed by this time (Fig. 6*b*), as was stated expressly by Guérin.

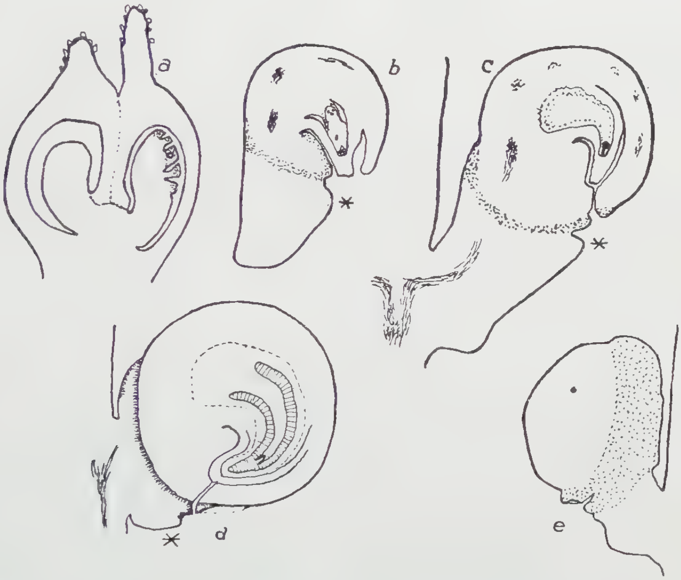

Fig. 6. *Cardiospermum halicacabum. a-d.* Sections of ovules and seeds of successive age, at different magnification. *a.* Gynoecium in young flower bud, *b.* in open flower, *c.* some time after fertilization, with the meristematic tissue of the developing arillode dotted, *d.* almost mature seed with the two layers of the arillode hatched, *e.* ovule shortly after fertilization, seen from the side, with the nearly white arillode dotted.

Obviously because he was convinced that every ovule must have a funicle and that an "aril" originates from a funicle, Kadry drew the attention to a bulge found between the micropyle and the placenta (which bulge is in fact the outgrowth of the placenta which acts as a funicle) which is present before fertilization and would according to him develop into an aril. According to him this bulge (indicated by an asterisk in my figures) is an outgrowth of the funicle, which later on surrounds the micropyle as well. At this place inside the curvature the outer integument, though recognizable in young ovules, is said to become undistinguishable in older ovules. We can, however, discern it in his drawing, and it is clearly recognizable in Guérin's drawings as well as in my own sections (Fig. 6). The part of the outer integument situated inside the fold shows in a section through the plane of symmetry the semi-circular shape that is so characteristic for the *Sapindaceae.*

The "aril" is certainly not, as said by Kadry, an extra-layer fused with the testa (outer integument). Apart from direct observations to be described further on, the arguments against this view are the same as those given in our discussion of the corresponding part in the seed of *Paullinia.* In mature seeds we see in the transition zone between the white "aril" and the dark "testa" that the latter has a typical dark pallissade epidermis with thick outer walls, and that in the "aril" this layer (and only this layer) is replaced by a several-layered tissue of thinner, colourless cells. In the immature seed of Fig. 6*d* the central part of this tissue is divided into two layers because the cells in its middle have become large and thin-walled.

The second and deeper layers of the dark-coloured part of the testa extend uninterrupted through the transition-zone and pass into similar layers across the chalazal region. Underneath "aril" and unchanged epidermis of the dark testa these deeper layers are in the ripe seed equally hard and dark.

The "aril" is sometimes said to cover the micropyle. In fact, and this is just as important as it is in *Paullinia*, the micropyle is not covered. In unripe seeds it is visible on the outside near the margin of the arillode. The several-layered epidermis extends a little way beyond the micropyle.

My own investigations show that the description and interpretation given by Kadry have to be amended in several more points.

There is no thin, true funicle as figured in Kadry's Fig. 14. The figures in Payer's "Organogénie" (1857) already proved this. From the beginning the ovule is inserted with a broad base on the typical outgrowth of the placenta. This outgrowth, which functions as a funicle, has the same texture as the carpel wall and contains the same, heavily colouring idioblasts.

The outgrowth forms a brownish bulge below the ovule. That it looks as if this bulge grows out over the ripening seed, is due to the fact that internal changes in the arillodal part of the testa (splitting of its layers) proceed upwards, so that it looks as if the brownish colour of the bulge on the outgrowth of the placenta spreads upwards. The outgrowth of the placenta itself does not develop any further.

My sections (Fig. 6) show that the fertilized ovule develops an arillode from the usual regions near the micropyle indicated in Fig. 1.

Whereas the main part of the ovule is covered by a typical epidermis with smooth cuticle, and underneath the epidermis with parenchymatous tissue, the parts of the integument which are dotted in Fig. 6 remain for a longer time meristematic; they are rich in protoplasma, consist of very small, thin-walled cells, and show an uneven surface. The meristematic region between ovule and pseudo-funicle, clearly belongs to the integument, even in the raphal region.

The outer integument also produces a meristematic bulge situated between micropyle and pseudo-funicle. During anthesis (Fig. 6*b*) this bulge is still united with the part inside the fold of the inner integument which later on is separated.

Seen from the outside this arillode is clearly distinguishable in young seeds, as shown in Fig. 6*e*, which represents a slightly older stage than Fig. 6*b*. The colour of the arillode is nearly white and dull, whereas the rest of the testa is brown and glistening.

The arillodal region is traversed by a single vascular bundle, which might be regarded as a raphal bundle. However, shortly after entering the outer integument above the arillodal layer, it divides into two branches, one on each side of the median plane, and the latter split into several bundles.

In larger seeds the greater portion of the nucellar part (the radicular pocket) does not show the arillodal development of the epidermis, and forms the black notch that penetrates in the white, heart-shaped arillode.

The tissue of the arillode does not become fleshy, and it differs, therefore, in this respect from what I regard as the original condition in the *Sapindaceae*. Its different character is apparently connected with a change in the way of dispersal, which is no longer zoöchorous. The arillode persists, but functions merely as an abscission layer.

In herbarium material in which ripe seeds are present, it is easily seen that the outer layer of the arillode is separated from the inner one. The outer layer remains attached to the placenta and the inner layer to the seed. It forms the white mark, which can easily be scratched off. So the white heart-shaped mark is not something sticking to the testa, but a scar, i.e. a place where something is missing. This remnant of the arillode is a pseudo-hilum, comparable to that described for *Paullinia*, etc.

Euphoria (*Nephelium*) **longana** Lamk. (*Nephelieae*)

Radlkofer (1895) considered the fleshy, edible layer round the seed as a free aril. This interpretation looks plausible as the "aril" arises at the base of the seed from a narrow ring which contrasts by its white colour with the brown testa.

The ring remains dormant for a long time after fertilization. In fruits of 2.5 cm length i.e. in a fairly advanced stage of development (seed 1.6 cm) the ring is 2.5 mm high, in another fruit of 2.9 cm length the "aril" has grown out to $^1/_3$ the length of the seed, in an almost ripe fruit of 3.5 cm length the "aril" entirely surrounds the seed and overlaps the top with its lobes.

I could study the nature of the ring in sections.

In young ovules (Fig. 7*a*) a situation is found resembling that in *Cupania*. The horizontal body below the ovule is easily recognizable as a fold of the carpel. Its epidermis is continuous with the internal lining of the latter, and its subepidermal layer contains the same kind of idioblasts as the corresponding layer on the inside of the pericarp. It has a double layer of vascular bundles, the upper one connected with the bundles of the central axis, which below the plane of section pass into the style, the lower one connected with more peripheral bundles in the torus. There are, however, anastomoses between the two.

The ovule proper is here too inserted with a broad base, and consists of a different kind of cells.

The situation is schematically represented in Fig. 7*b*, where the pseudo-funicle is interpreted as an outgrowth of the "*Querzone*", the rim of the lower, peltate part of the carpel, which is horizontally incurved. This ovary would differ therefore from those found in many other families, where the ovules are borne in vertical rows on or near the margin of the upper carpel parts.

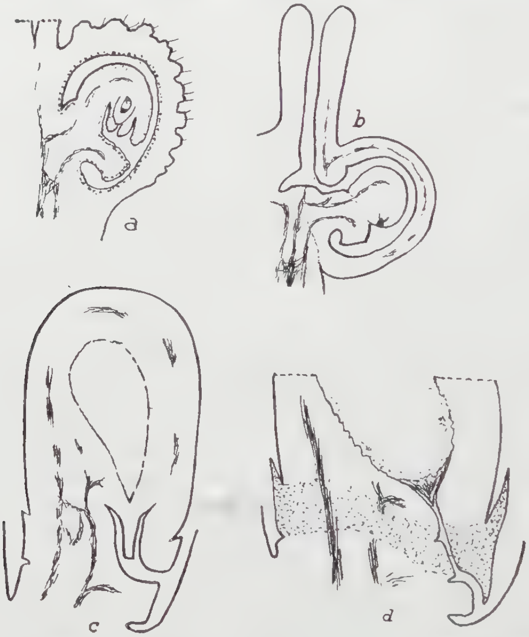

Fig. 7. *Euphoria longana*. *a*. One cell of the ovary of an open flower, *b*. Schema of the structure of an ovary cell, *c*. young seed of 3½ mm length, *d*. basal region of young seed of 5 mm length; arillodal region dotted.

Fig. 7*c* represents a longitudinal section of a young seed of 3.5 cm length. Above the groove between seed and pseudo-funicle the white ring which is to grow out into the arillode, is visible; it is separated from the rest of the seed by a second groove. The ring is a differentiation of the outer integument and runs internally from its tip across the seed to the chalazal region; therefore a typical arillode. The upper part of the seed has a one cell thick, smooth epidermis, whereas in the arillode the epidermis, just as in *Cardiospermum*, is not sharply delimited.

In older seeds, like that of Fig. 7*d*, the ring grows out in an upward direction. The tissue remains white and soft (dotted in Fig. 7*d*). At the micropylar side of the seed the ring extends beyond the micropyle, which is so well hidden by it that it is difficult to find, except in microtome sections. When the seed is detached from the basal part of the arillode, it exhibits a pseudo-hilum.

The campylotropy of the ovule is but weakly expressed, and in the seed it is no more recognizable, as the endosperm in the embryonic sack develops, just as in *Nephelium*, in a longitudinal direction only.

Litchi chinensis Sonn. (*Nephelieae*)

The genus *Litchi* has according to RADLKOFER (1933) a free aril. In the drawing given by RADLKOFER in 1898 (Fig. 167*B*) the "aril" is wrongly represented as fully closed around the seed, while in fact it is open at the top between the overlapping folds.

The "aril" develops just as in *Euphoria* from a white ring round the base of the seed. It takes here even longer before it grows out than it does in *Euphoria*. In fruits of 2.5 cm with seeds of 1.6 cm length the ring was 2.5 mm high, whereas in fruits of 2.9 cm with seeds of 1.9 cm it covered one third of the seed. Only in almost mature fruits of 3.5 cm (seeds 2.3 cm) the "aril" had reached its ultimate size.

The question now arises again, of what nature the ring is.

BANERJEE (1944) gave a figure (his Fig. 13) with an "obturator" over the micropyle, and thought that from this organ and the likewise papillated tissue at the raphal side the aril might develop. I could confirm the presence of these tissues, but am certain that the "obturator" is the usual outgrowth of the carpel, here covered with papillae. It does not develop any further (Figs. 8*a* and 8*d*), and is still recognizable in rather large seeds as a white parenchymatious tissue situated under the meristematic ring.

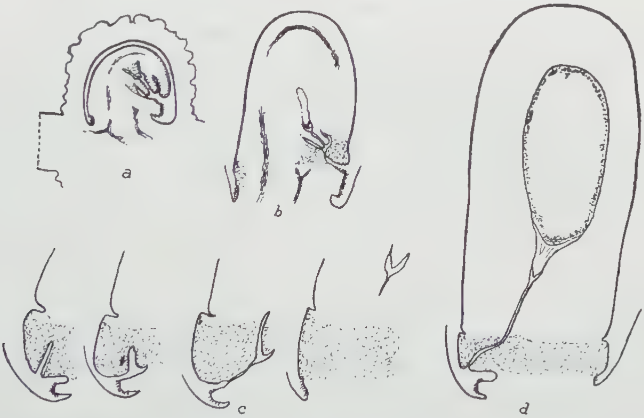

Fig. 8. *Litchi chinensis*. *a*. one ovary cell of open flower, *b*. ovule considerably swollen, *c*. subsequent sections through the micropylar region of a young seed forming part of a series, *d*. seed of ± 1 cm length; endosperm freenucleate.

Some time after fertilization (Fig. 8*b*) the outer integument appears to be distinctly swollen at the places *a*, *b* and *c* of Fig. 1. At the place *b* the thickening is still diffuse. In older seeds the zones *a* and *c* have differentiated outwardly into the protruding ring of meristematic tissue that we found also in *Euphoria*, whereas the rest of the seed is covered by a smooth epidermis. The ring is separated from the main part of the integument by a groove. The micropyle lies below the ring. If the latter were an aril, the micropyle should lie above it. The ring is clearly the narrowed partial sarcotesta predicted in the description of *Paullinia*.

In the vicinity of the micropyle part *b* of the outer integument also grows out, so that in this region the ring consists of a double layer (Fig. 8*c*). The inner integument remains as a cap much higher in the seed, as shown in the schematic drawing given in Fig. 8*d*.

The cup which develops out of the ring is, just as in *Euphoria*, an arillode. From the rim of the outer integument it extends to the raphal side. The ripe seed shows (in contrast to what we find in an arillate seed) the micropyle inside the pseudo-hilum (cf. Fig. 12).

Toechima plurinerve Radlk. (*Cupanieae*)

A figure of a longitudinal section through an almost mature fruit is given in Fig. 9.

The seed seems to be attached with a wide base to the placenta, i.e. without the intermediary of a funicle. At its base it is enveloped by a yellow, fleshy ring (dotted in the drawing).

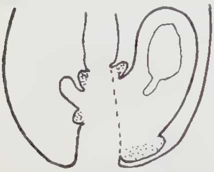

Fig. 9. *Toechima plurinerve.* Longitudinal section of almost ripe fruit with one ovule aborted. Arilloid dotted. Detachment along interrupted line.

Radlkofer (1933) describes this situation as follows: "supra hilum transverse dilatatum arillo brevi spurio pericarpio instructa".

As long as we have not studied its development, it is impossible to decide the question of the morphological mature of this arilloid; it may be a product either of the micropylar region, of the rudimentary funicle, or of the placenta.

The yellow ring remains attached to the seed, when the latter is shed.

Didierea

The genera *Didierea* and *Alluandia* are classified by Perrot and Guerin (1903), as a, somewhat aberrant, group of the *Sapindaceae*. The structure of the ovules supports this view. Other authors, however, exclude them from the family.

Perrot and Guérin give a drawing of a longitudinal section (their Fig. 7) through a seed, and mention a small aril arising from the funicle, near the micropyle. As it is attached in the notch of the seed at the side of the radicula (and micropyle), it seems more probable that this "aril" originates from the integument. A comparison with their Fig. 3, which represents a mature ovule, confirms this view. We find here at the corresponding place, which corresponds also with area *b* of our Fig. 1, an outgrowth of the outer integument.

Pometia pinnata Forst. (*Nephelieae*)

The ripe seeds are surrounded by a fleshy layer. Radlkofer (1933) regarded the latter as an adnate aril. Corner followed him.

My material contained young fruits and unswollen ovaries. The latter were obviously derived from unfertilized flowers, as sections (Fig. 10*a*) show that their ovules are already degenerating. These ovules, however, give a good idea of the various layers in the mature stage, and show that the campylotropous curvature has at this stage not progressed very far. The nucellus has been resorbed by the embryosac, by now also obliterated, though in the remaining, basal part of the nucellus the cavity in which it was originally enclosed, is still recognizable. In the shrivelled apical part of the embryosac the egg apparatus may still be visible. Cross sections through the micropylar region show the presence of a micropylar canal.

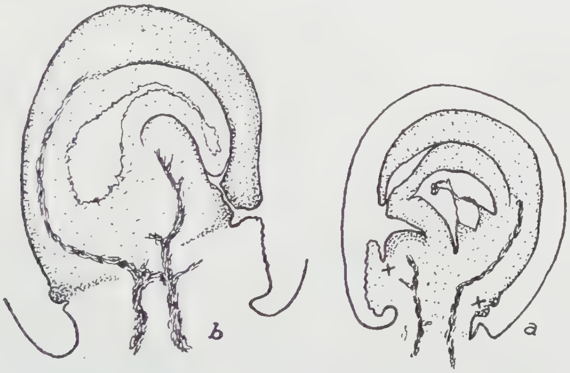

Fig. 10. *Pometia pinnata* ovules, *a*. mature, degenerating, unfertilized, *b*. from young fruit, less strongly magnified.

The ovule is, just as in other *Sapindaceae*, attached with a broad base, i.e. without a proper funicle. Some separate strands enter from the placenta into the basal part. The boundaries between placenta, funicle and ovule are as vague as in *Nephelium*, *Cupania*, etc., so that it is uncertain whether the part that looks like the base of the ovule really belongs to the latter.

Inside the notch between the micropylar and the chalazal part of the ovule the outer integument is represented by the typical, semicircular, bulge. Further we recognize in the section on both sides an outgrowth which represents a part of a tissue ring separated from the rest of the ovule by grooves. The basal groove runs in Fig. 10*a* between the two crosses. The region below it may represent the outgrowth of the placenta (obturator), with which we have become familiar in the seeds of other genera.

In transverse sections of the fertilized ovules two parallel rows of strands, perpendicular to the median plane of the ovule, are seen to enter the ovule. The row at the right in Fig. 10*a* enters the outer integument splitting into many bundles. The bundles of the row at the left show some anastomoses with those of the row on the right, but remain mainly inside the enclosed part of the integument.

Fig. 10*b* represents a median section through an ovule a long time after fertilization. It had already increased to twice its original size. The basal part is especially rich in protoplasma, and reminds one of the arillodal ring found in other genera. This zone forms a disk which separates the seed from the placenta (dotted in Fig. 10*b*).

It seems plausible to assume that the mature seed will possess a fleshy "aril" developed from this meristematic tissue, and that it will later on be detached at this place from the placenta.

The outgrowth below this part (the obturator) shows no meristematic character. Its cells are large and uncoloured.

In herbarium material we found fruits up to 17 mm in length, with seeds up to 7 mm long. The latter showed as yet no distinct arillode. In the light of our observations on similar fruits of *Litchi* this does not mean that no arillode will develop.

Sapindus (*Sapindeae*)

This genus too is zoöchorous, but the edible part is no longer found in the seed. The pericarp has taken over the function of the sarcotesta and the arillode, and the fruit has become a berry. The testa is a very hard and dry protective coat.

Radlkofer (1895) was of opinion that the berries of the best-known species, *S. saponaria*, are not adapted for dispersal by animals. However, in a study of 1957 I could report that dispersal by bats has been observed in Trinidad as well as in Java. The detached seeds are probably spread by sea-currents too.

It would be worth while to see whether there are remnants of older conditions in the form of vestigial arilloids. This seems the more desirable as Mauritzon (1936*a*) gave in his Fig. 3*D* a section of an ovule of *S. mukorossi*, which shows the presence of an outgrowth below the ovule. The drawing is reproduced here as Fig. 11. Mauritzon obviously thinks that the outer integument is absent at the side of the "funicle", and that at this spot there is an outgrowth from the carpel which covers the micropyle, a kind of "obturator" therefore. There is no proper funicle, and the base of the ovule is in the well-known way broadly attached to the placenta. In several species the ripe seeds remain over some distance attached to the placenta, and when detached they show a linear scar. There is no aril, but sometimes a hair felt is found on seed and placenta.

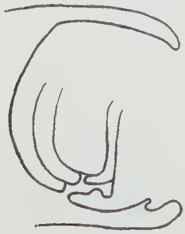

Fig. 11. *Sapindus mukorossi*, after Mauritzon.

Schleichera oleosa Merr. *(Schleichereae)*

There is a fleshy "aril" round the ripe seed. I could obtain no material for a study of its development. The way of attachment of the "aril", however, shows (Fig. 12) that the latter is an arillode, developed from the regions *a* and *c* in Fig. 1. It surrounds the micropyle,—just as in *Litchi.*

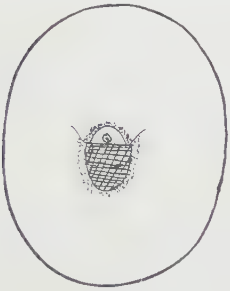

Fig. 12. *Schleichera oleosa.* Basal area of seed. Hilum hatched. Attachment area of arillode dotted.

Paranephelium (*Cupanieae*)

RADLKOFER (1933) remarked that the fruits and seeds of this tropical genus show a striking resemblance to those of *Aesculus.*

I saw fruits of *P.costophyllum* Miq. They have a hard, spiny pericarp, and the large brown seeds are provided with a partly smooth and partly dull testa. The dull part is often regarded as an aril, although it is just as hard and dry as the rest. RADLKOFER (1895) considered it as "*eine arillöse Schicht der Samenschale*".

The dull part of the seed is attached to the dissepiment. When the seeds are detached, the centre of the dull part shows as a remnant of the vascular strands a large, sunken scar, and herein the seed differs from that of *Aesculus.* Obviously the ovule had in its youth a very broad base with many bundles entering.

The place where the smooth surface penetrates for some distance into the dull surface, is the pocket in which the short radicle is hidden. The testa is here very thin, whereas the adjoining dull part is extremely thick.

C. CONCLUSIONS

Our observations on the seeds of the *Sapindaceae*, though limited to a few genera, have given us an insight into the nature of the arilloid structures occurring in the family. The majority of the tribes recognized by Radlkofer were represented in our material and the genera discussed here belong to the most divergent among them.

Our impression that the fruits in this family originally contained large seeds provided with a fleshy testa originating from the outer integument, was strengthened.

That such a sarcotesta may be present, had, as I remarked in the introduction, already been recognized by RADLKOFER (1895) in some of the genera. We found it now also in a *Nephelium* species, and we also discovered instances of incomplete sarcotestas (arillodes) in several other genera. In *Cardiospermum*, *Harpullia*, *Litchi*, *Euphoria* and *Paullinia* they had been described so far as arils arising from a funicle. However, no true funicle, and therefore no aril, is present in any of the plants investigated.

In some species of *Litchi* and *Euphoria* the meristematic part of the integument forms a ring, which grows out a long time after fertilization. The meristematic arillode extends from the top of the integument across the base of the ovule to the pseudo-funicle; this in contrast to a real aril arising from a true funicle. That the vascular supply makes a detour, entering into the fleshy part via the integument, also distinguishes the latter from an aril.

The connection with the so-called endocarp-aril of *Guioa* e.a. has not been investigated.

The non-dehiscent bladder-fruits with anemochorous and hydrochorous dispersal and the dehiscent fruits with small, dry seeds seem to represent side-lines of development. The latter have not been investigated here. The drupaceous fruits seem to be a later zoöchorous development.

It may seem strange that the morphological nature of so many sapindaceous table-fruits had so far not been properly investigated. As items on the list for future research parade other important table-fruits like *Blighia sapida*, *Diploglottis australis* and *Alectryon excelsus*. That their study has so long been neglected may be due to the false conviction that the fleshy parts are everywhere of the same kind and that they are adequately described by the term "aril".

It does not seem plausible to assume that the funicular, true aril is the arche-type out of which the fleshy structures found on the surface of the seed itself, arose by "adnation". An exostome-arillode seems to be morphologically different from a true aril. Returning to the question of the sequence in the series of structures mentioned in the introduction, I have to admit that a typological range of structures can be interpreted historically (if deemed necessary) in different ways; we can start at any point. This does not mean, however, that we should refrain from every historical interpretation; this seems the less desirable as others have already proceeded in this direction.

Of course, transfer of functions between various layers may have taken place. A transfer of function from endocarp or aril to testa is here, however, morphologically improbable. It seems plausible to regard the undifferentiated, complete sarcotesta as the starting point for the development of more localized and specialized structures, which seem ecologically better adapted for dispersal by birds, as they are more easily detached.

Notwithstanding this differentiation in structure, we recognize in all of them (aril, endocarp-pulpa, arillode, sarcotesta) the original sarcotesta-function, viz. that of presenting an edible layer inside the purely protective pericarp.

At an earlier occasion (1955) I tried to find a historical background for the presence of this condition in various group of *Angiosperms* by regarding it as the persistance of a condition that occurred already in the seed of *Gymnosperms*.

Possible implications of our finds for the subdivision of the family may be left to taxonomists. The pluriformity in fruits and seeds seems to some extent to be independent of the accepted taxonomical delimitations, as it may vary even within genera. The gap between *Nephelium* and *Euphoria* nevertheless seems to be widened by our finds.

In the ovules and seeds themselves we found once more that the campylotropy may appear at a comparatively late stage in the development, and that some of them retain the campylotropous structure permanently by developing in a transverse as well as in a longitudinal direction, whereas others loose it by developing mainly in a longitudinal one.

As an argument for the primitiveness of the sarcotesta I wish to draw the attention to its presence in groups in which other characters occur that are primitive. In my general study (1955) I reported the presence of such a correlation in various families belonging to the *Monocotyledones*, viz. in many *Liliaceae*, *Amaryllidaceae* and *Iridaceae* as well as to the *Dicotyledones*, viz. in *Degeneriaceae*, *Magnoliaceae*, *Ranunculaceae*, *Winteraceae*, *Annonaceae*, *Berberidaceae*, *Connaraceae* and in some primitive *Leguminosae*.

On the other hand I have to admit that in the *Sapindaceae* this character may have arisen anew, and that is may be here merely a parallel to the *Gymnosperm* condition, one note in the extensive gamma of means the family uses to attract dispersers. That it is no primitive character in the *Sapindaceae* may seem indicated by the wide range of fruits found in this family and the rather advanced position of this family in the natural system, where the families in the various taxonomical groups are often arranged in a rectilinear sequence. When we accept the position of the family at the end of the series *Ranales-Rosales-Malvales-Tricoccae-Geraniales-Rutales*, we should, however, not overlook that a sarcotesta and structures derived of the latter occur also in some of the "intermediate" families, viz. the *Sterculiaceae*, *Bombacaceae*, *Euphorbiaceae* (very pronounced here), *Oxalidaceae*, *Polygalaceae*, *Tremandraceae* and *Meliaceae*, as well as in the "succeeding" member of the series, the *Celastracaeae*. This does not plead for a development de novo.

Sporne (1945) gave a new, revolutionary arrangement of the families of the *Angiosperms*, based on the statistical frequency of "primitive" characters as expressed in his "advancement index". The *Sapindaceae* are there placed very low, as the eighth from below of the dicotyledonous families.

As this arrangement rests inter alia on the seed-characters (seeds arillate, seeds few, integument bundles present) its reliability depends partly on the acceptability of the opinion that the arilloid testa of the *Sapindaceae* should be considered as a primitive character and not as an incidental, i.e. secundary, adaptation, viz. to zoöchorous dispersal.

Sporne himself remarked that two of his other criteria, viz. "apetaly" and "small number of seeds" are in themselves not reliable indicators of advancement, because they may occur *a*) as ancestral characters in very primitive groups, and *b*) as the result of a process of retrogression in some very advanced families. The combination of the two characters forms, as already indicated by Stebbins, an"adaptive peak", indicating anemophily. It is clear therefore that *a*) and *b*) refer to resp. primary and secundary anemophily.

Considering all this, and recognizing that arilloid structures are often parts of the integument, it seems necessary to point out that the correlation found by Sporne between the characters "seeds arillate" and "integument bundles present", does not necessarily prove them to be both primitive ones. As I tried to show for the seeds of the *Sapindaceae* the correlation may be due to ecological factors (see below). Whether they may at the same time be regarded as primitive characters, is an independent problem.

Another point of general interest is that the pseudo-funicle, as MAURITZON (1936*a*) already indicated for *Dodonaea*, is, as a rule, wholly or partly an outgrowth of the carpel wall. A true funicle is usually absent. The ovule is attached with a broad base, it is without a raphe and provided already at the very base with several vascular bundles.

Vascularitation of the ovule by several bundles is exceptional in the *Angiosperms*. As far as I know the phenomenon is limited to some ovules of sea-shore plants as *Hymenocallis occidentalis* and *Typhonium lindleyanum*, where it may be correlated with definite ecological needs, viz. resp. water-storage in the testa and germination of viviparous seeds. In the plants investigated here there is also a special need in the strongly developing integument. It is noteworthy that especially in *Litchi* and *Euphoria* the water supply to the succulent arillode has to make a detour via the integument up to its micropylar region.

The boundary between ovular and placental tissue is rather vague, and it is therefore no wonder that the place of attachment of the seed sometimes grows out with the placenta, a phenomenon usually called adnation, but which may perhaps better be indicated as nondisjunction of placenta, pseudo-funicle and seed.

The situation in the *Sapotaceae* shows some resemblance to that in the *Sapindaceae*, and its development deserves a special study. There too the micropyle is often situated inside a large "scar", the "*Ansatzfläche*" or "area umbilicalis".

D. AESCULUS

We will discuss the seeds of the genus *Aesculus* in connection with those of the narrowly related *Sapindaceae*. The structure of the latter may shed light on the rather unusual aspect of the first. The genus may be regarded as a northern outpost of the tropical *Sapindaceae*. It has a near relative in the tropical genus *Billia*.

The seeds of *Aesculus* are large, but the outer integument, although at first strongly developed, changes later on as a whole into a hard, dry testa. They may remain for a long time dormant, but possess no special dispersal mechanisms, a situation also met with in *Paranephelium*.

The European species, *A. hippocastanum*, was driven southwards by the last glaciation, and did since then not recover its former area, although the climate in N.W.-Europe is not unfit for it. This may be due to the absence of special means of dispersal. The seeds of the related tropical-American genus *Billia* are said to be provided with an aril (cf. Corner (1953). Alas these seeds were not obtainable.

The first feature that strikes us in the seed of *Aesculus*, is the very large "hilum". Though some textbooks call it a "macula hilaris", most of them simply refer to it as a hilum. The micropyle is situated just outside the hilum, so that the radicular pocket also ends outside it, a situation often misrepresented in the literature.

The outer surface of the radicular pocket lies as a whole outside the "hilum"; it often forms a triangular notch in the latter's dull surface, just as in some *Sapindaceae* with a bilobate pseudo-hilum. This fact, together with the large size of the hilum, suggests that the "hilum" may in reality be the scar of a detached arillode, a pseudo-hilum.

On the other hand the dull spot also is the place where the seed originally was attached to the dissepiment.

It is, therefore, noteworthy that shortly after fertilization a funicle seems to be present (Fig. 13). This "funicle" is separated from the ovule proper by a deep transverse groove. The funicular part is often greenish, whereas the ovular part proper is white.

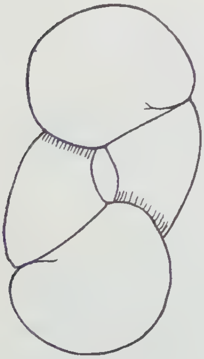

Fig. 13. *Aesculus hippocastanum*, two ovules from opened ovary cell attached to underlying placenta, shortly after fertilization.

These seemingly contradictory facts require a closer inspection. The situation in the ovary then appears to be complicated by fusions and bends. In the study of Kayser (1893) this has been well analysed. We derive from it the following details:

The ovules are inserted on the dissepiment and not in the axil of the ovary cell (Fig. 14). Popularly said the basal part of the funicle seems to be fused with or incorporated into the dissepiment. This situation is already anticipated in many *Sapindaceae*, where the so-called funicle seems to belong at least partly to the wall of the carpel. On transverse sections of the ovary which I made myself, the vascular bundle of the ovule appears to arise from the axillary strands of the placenta. It runs more or less horizontal through the dissepiment and leaves the latter halfway.

In Kayser's Fig. 1, a transverse section of the ovary, the basal part of the obliquely cut ovule, the pseudo-funicle, appears to be broadened laterally, and to form a distinct part.

My own transverse sections (Fig. 14) show that this part, which contains an undivided vascular bundle, consists, before fertilization, for the greater part of a large-celled, rather loose parenchyma of a similar kind as that in the pericarp, whereas the apical, nucellar part consists of a denser tissue.

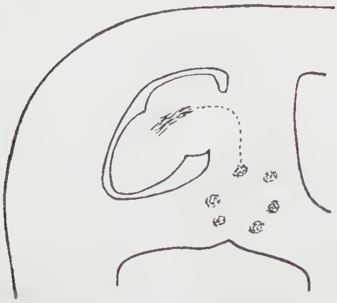

Fig. 14. *Aesculus octandra.* Cross section of ovary in anthesis. Course of strand outside plane of section indicated by dotted line.

Kayser's drawing of longitudinal sections of the ovule (cf. her Fig. 3), which fully agree with my own ones, have one shortcoming, viz. that they do not represent the entire basal part and the course of its bundle, which gives the impression that the nucellar part is the entire ovule and that the funicular part is the placenta. It seems necessary to add that the vascular bundle in the funicular part is unusually stout and seems compound. It forks into two branches in the ovule proper. These two branches split into a number of parallel strands which pass into the outer integument.

Fig. 96 of Kühn (1927) gives the same wrong impression.

The neglect of the funicular part in the description of sections is caused by the circumstance that it stands perpendicular to the symmetry plane of the ovule proper, which means that the latter is attached more or less laterally. In a longitudinal section through the symmetry plane of the ovule the funicular part, therefore, is missing.

In Fig. 15 I reconstructed by the aid of a number of longitudinal and transverse sections a scheme of the structure peculiar to the ovule of *A. octandra* and *A. hippocastanum.*

It is clear that the green, basal part is not an ordinary funicle, but that it is homologous to the "obturator", the outgrowth of the carpel found in the *Sapindaceae.* In its central zone it is not delimitated from and may contain tissue of the outer integument by a kind of fusion and contraction. Internally it may thus have become more or less arilloid, but at the periphery it is morphologically not comparable to the arillode of *Litchi* and its allies. This complex mass is separated from the nucellar part, the ovule proper, by the groove mentioned above and indicated in Fig. 15 by a dotted line. This groove is in my opinion comparable to the first, basal groove in *Pometia*, *Litchi*, etc.

The fusion of obturator and integument into a single mass is perhaps less complete in the ovule of its tropical relative *Billia*, and in that case the integumental part may be developed into an arillode, which remains attached to the seed at maturity.

The vascular supply of placenta and ovules in *A. parviflora* has recently been described by BAEHNI and BONNER (1953). Their Fig. 1 shows the origin of the ovular bundle from an axillary strand, after which it runs through the dissepiment. They believe in a fusion between the funicle and the dissepiment. One difference with the situation I noted in *A. hippocastanum*, is very interesting. The bundle in the "free part of the funicle" gives off a number of short branches. The authors say that this branching inside the "funicle" seems strange, but becomes comprehensible when we realize that part of the "funicle" may be regarded as arilloid.

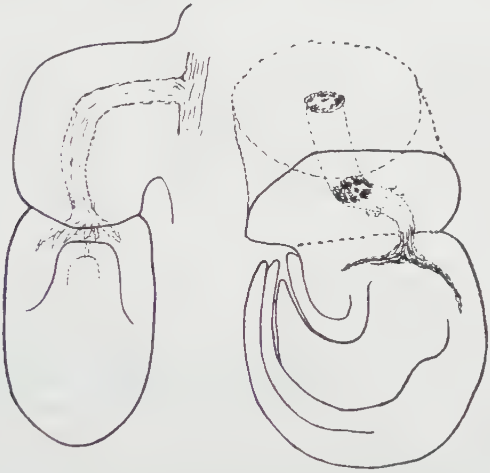

Fig. 15. *Aesculus*. Right: longitudinal median section of inferior ovule fully drawn. Vascular bundle and basal part of ovule outside plane of section in dotted lines. Left id. from the side.

When we compare this situation with that found in the *Sapindaceae*, and when we see that the ovule, attached by the broad, partly arilloid outgrowth to the dissepiment, develops in conjunction with the latter, we can understand the situation in the ripe fruit.

The parenchyma developing in the arilloid does at first not differ from the tissue of the dissepiment. In the ripe fruit, however, the arilloid is recognizable as a thin, but distinct part. When the seed is detached, the greater part of the arilloid remains behind as a distinct bulge on the surface of the dissepiment (Fig. 16)—just as part of the arillode remains behind on the placenta of *Cardiospermum*. It is cream-coloured in contrast to the rest of the surface and has a different consistency, viz. soft and mealy. In its center we see the scar where the single vascular strand has been broken off. The course of the vascular strands passing into the seeds is then visible in the dissepiment to the naked eye.

At maturity the hardened layer of the testa which separates the seed from the obturator, is detached from the mealy layer, as described already by Hintzinger (1927, p. 260). It has now become clear that by the absence of a raphe and a funicle and by the fusion of integumental and placental tissue into one layer, the scar may as well be described as a hilum as a pseudo-hilum and that the term "hilum" is here even no longer applicable.

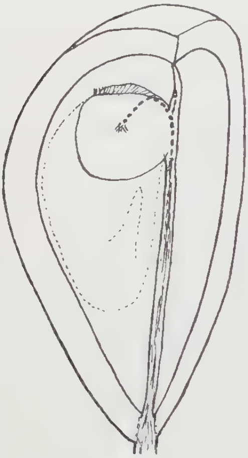

Fig. 16. *Aesculus pavia.* Fruit valve seen from the inside, with area where seed was attached in front. Vascular bundle in dissepiment coarsely dotted. Contour of seed finely dotted.

When we consider the structure of the testa from the ecological point of view, the completely sclerified testa may be seen as an adaptation to a life in extra-tropical regions. Still more clearly than the dry arillode of *Cardiospermum*, the contracted arilloid obturator has as the end of a line of development lost every zoöchoric importance, and has become an abscission layer.

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LES PELOUSES SÈCHES DES DUNES DE LA CÔTE NÉERLANDAISE

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1. Introduction

Le long de la côte néerlandaise s'étend une zone de dunes, particulièrement séduisante, interrompue seulement à Petten sur une longueur de quelques kilomètres. Entre Scheveningen et Schoorl, soit sur une distance de 75 km, la largeur de la zone des dunes n'est nulle part inférieure à 2 km, et elle atteint même 5 km à Haarlem. Ce cordon dunal se prolonge, d'une part en direction NE dans les îles néerlandaises et allemandes de Wadden, et finalement le long de la côte occidentale du Danemark, d'autre part en direction SW dans les îles des estuaires du Rhin, de la Meuse et de l'Escaut, et ensuite, quoique la largeur du cordon soit ici généralement plus étroite, le long des côtes de la Belgique et du Nord de la France. Ici le paysage des dunes cède graduellement la place aux falaises côtières, et en Normandie et en Bretagne on ne trouve plus que des petites zones de dunes isolées.

Les dunes des côtes néerlandaises ont été formées à-peu-près entre 300 et 1000 après J.C., en partie devant l'ancien paysage des dunes, en partie sur l'emplacement des anciennes dunes. (Jeswiet, 1913; Tesch, 1920–30).

Ces deux paysages de dunes sont, en principe, nettement distincts au point de vue topographique; d'autre part, aux points de vue de la géomorphologie et de la végétation, ils possédaient en général un caractère tout à fait particulier. Cependant au cours des siècles, l'ancien paysage des dunes a été mis en culture, souvent d'une manière intensive, de sorte qu'actuellement, il est à peine reconnaissable pour le non-initié, en de nombreux endroits, notamment là où le sable a été enlevé en faveur de la culture des tulipes. Aussi, lorsque nous parlerons des "dunes", viserons nous généralement le paysage récent.

On peut distinguer, au sein de l'ensemble du paysage des dunes, les dunes situées au N de Bergen (y comprises les dunes des îles de Wadden), de celles situées au S de Bergen, et pour lesquelles van Soest (1929, 1952) créa les termes de "District de Wadden" (Waddendistrict) et "District des Dunes" (Duindistrict). Le District de Wadden se distingue du District des Dunes, entre autres par la présence d'espèces à aire surtout boréo-atlantique. Ainsi *Calluna vulgaris* et *Empetrum nigrum* y jouent un rôle important dans la végétation. Par contre, dans le District des Dunes, on note un grand nombre d'espèces à distribution plus atlantique-méridionale, (sub)-

méditerranéenne ou médio-européenne (par ex. *Silene conica*, *S. nutans*, *Carlina vulgaris*, etc.).

A côté des groupements végétaux, typiques pour toute la zone maritime, et qui rélèvent des alliances de l'*Ammophilion* et du *Koelerion*, on peut exprimer phytosociologiquement la différence entre les deux districts de la manière suivante: dans le District de Wadden, ce sont des types de végétation relevant des *Corynephoretalia*, *Calluneto-Ulicetalia*, éventuellement des *Quercetalia roboris-sessiliflorae* qui dominent; par contre dans le District des Dunes, les *Brometalia* et *Prunetalia spinosae* jouent un rôle très important.

Les différences spectaculaires entre les Districts de Wadden et des Dunes, s'expliquent par la teneur en carbonates du sable des dunes. Dans le District de Wadden, cette teneur en carbonates, toujours inférieure à 1 %, est le plus souvent en dessous de 0,2 %; dans le District des Dunes, cette teneur varie entre 2,5 % et 4,5 %, mais peut éventuellement atteindre des valeurs bien plus élevées (VAN DER SLEEN, 1912; JESWIET, 1913; BIJHOUWER, 1926). Quoique la flore et la végétation de tout le paysage ancien soient très voisines de celles du paysage récent des dunes au N de Bergen, on applique cependant la distinction entre Districts de Wadden et des Dunes également à l'ancien paysage.

On peut constater avec satisfaction, que malgré la forte densité de la population de notre pays, le paysage des dunes néerlandaises a été jusqu'à présent et dans la plupart des cas, peu altéré par l'homme, au contraire de ce que l'on observe à la côte belge. Quoique la flore se soit appauvrie à plus d'un égard, depuis 100 ans, suite à un assèchement des dunes, une région très intéressante et très belle a été conservée dans son ensemble, non seulement quant au paysage, mais également quant à la flore et la végétation.

Il n'est donc pas étonnant, que beaucoup de botanistes hollandais aient choisi les dunes, comme objet de recherches (van Eeden, Vuyck, Jeswiet, etc.). BIJHOUWER (1926) le premier, fit des recherches orientées sur la végétation, tandis que de Leeuw se consacra à l'étude de la végétation des dunes vers 1930.

Ces travaux, ainsi que ceux de plusieurs autres botanistes (Braun–Blanquet, Weevers, Westhoff, Meltzer) trouvèrent leur aboutissement dans la discription de plusieurs groupements végétaux; citons parmi ceux-ci, les pelouses sèches suivantes, que nous étudierons de plus près:

1. *le Tortuleto-Phleetum arenarii* Br.-Bl. et de L. 1936,
2. l'association à *Festuca capillata* et *Galium maritimum* Br.-Bl. et de L. 1936 (désignée par la suite comme *F.-G.*),
3. l'association à *Anthyllis maritima* et *Silence otitis* de L. 1938 (désignée comme *A.-S.*),
4. l'association à *Anthyllis vulneraria* et *Trifolium scabrum* Weevers 1940 (désignée comme ass. à *Anthy. v.* et *Trif. sc.*),
5. le *Violeto-Corynephoretum dunense* Westhoff 1943.

Après la deuxième guerre mondiale, plusieurs recherches phytosociologiques approfondies, furent de nouveau consacrées à plusieurs de nos régions. Entre autres, l'auteur eut l'occasion, au cours des années 1952, 1954, 1955 et 1956, d'étudier d'une manière intensive, la région des dunes de la "Haagse Duinwaterleiding", c.à.d. la zone située entre Scheveningen et le Wassenaarse Slag, large de 2 à 3 km, et longue de 6 km. En même temps, diverses autres régions de la zone côtière néerlandaise, furent explorées.

Au fur et à mesure de la progression des recherches sur les groupements des dunes, et de l'accumulation des relevés provenant d'autres régions, la nécessité se fit jour, d'individualiser les différentes associations d'une manière plus précise; d'autre part il a été possible de reviser la classification, ou de la compléter. Les difficultés les plus importantes ont été rencontrées dans les types de végétation fermée; c'est à ceux-ci que sera consacré le principal de cette étude, tandis que nous ne parlerons qu'en passant du *Tortuleto-Phleetum* et du *Violeto-Corynephoretum.*

L'élaboration de cet aperçu des pelouses sèches est basée sur les relevés déjà publiés de Braun-Blanquet, de Leeuw et Weevers, sur nos propres relevés, et également sur l'importante documentation inédite de de Leeuw, Westhoff et Doing Kraft.

2. L'ANTHYLLIDETO-SILENETUM de L. 1938

C'est en raison de la place centrale, occupée par l'A.-S., dans l'ensemble des formations herbeuses des dunes néerlandaises, que nous commençons notre examen par cette association.

Déjà en 1934, DE LEEUW mentionna, dans la région des dunes hollandaises au S de Helder, un groupement végétal "riche en espèces du Bromion", sans pousser l'analyse plus loin. Ce groupement était conçu d'une manière très large: il comprenait l'*Anthyllideto-Silenetum,* décrit quelques années plus tard par de Leeuw, et l'association à *Anthyllis vulneraria* et *Trifolium scabrum* des digues des îles sud-hollandaises et zéelandaises, décrite en 1940 par Weevers. Ce groupement du *Bromion,* fut incidemment appelé en 1936 "*Cerastieto-Avenetum*" (Braun-Blanquet, etc.). En 1938, DE LEEUW créa le nom: association à *Anthyllis vulneraria maritima* et *Silene otitis* pour les groupements des pentes exposées au N et à l'E des dunes calcaires.

Simultanément à cette dernière publication, parut le fascicule du "Bromion erecti" du Prodrome des groupements végétaux (BRAUN-BLANQUET et MOOR, 1938) ou l'association est décrite en détail. Le Prodrome signale l'*A.-S.* dans les dunes calcaires de la côte néerlandaise, dont la distribution est donc cantonnée dans le District des Dunes. Le groupement trouve son développement optimum, selon le Prodrome, dans la région située entre Noordwijk et Scheveningen, particulièrement aux expositions N, NW en NE. Braun-Blanquet et Moor citent comme caractéristiques d'association (par ordre de présence décroissante): *Arabis hirsuta* (L) Scop., *Anthyllis vulneraria* L. ssp. *maritima* Schweigger, *Botrychium lunaria* (L) Sw. *Satureja acinos* (L.) Scheele, *Carlina vulgaris* L.; *Silene otitis* (L.) Wibel, *Thalictrum minus* L. var. *dunense* Prod., *Viola rupestris* F. W. Schmidt, *Gentiana cruciata* L., *Euphrasia parviflora* Schagerstr. ssp. *glabrescens* Wettst., *Orobanche picridis* F. W. Schultz, *O. purpurea* Jacq. et *Artemisia campestris*

L. ssp. *maritima* Lloyd. La plupart des espèces caractéristiques citées par le Prodome peuvent à notre avis être considérées comme telles, du moins localement; dans ce cas elles ne prêtent pas à discussion. Faisons cependant les remarques suivantes au sujet de quelques unes d'entre elles.

a. *Viola rupestris.* L'espèce semble être la plus répandue dans les dunes entre Scheveningen et Katwijk et atteint ici un optimum marqué dans les groupements de vallée, où *Festuca ovina* domine. Nous ne rapportons pas ces groupements à l'*A.-S.*; nous y reviendrons dans le chapitre suivant.

b. *Satureja acinos* est certes localement assez abondant dans l'*A.-S.*, mais est tout aussi fréquent dans les groupements de vallée cités dans le *a*) ci-dessus, cependant qu'il semble montrer une certaine préférence pour les groupements incomplètement fermés.

c. *Artemisia campestris* ssp. *maritima* est lié aux groupements ouverts des dunes, et est plutôt une caractéristique locale du *Tortuleto-Phleetum* que de l'*A.-S.*

d. *Silene otites* est au total une espèce assez rare dans le District des Dunes, qui localement est plus abondante. L'espèce est toujours notée dans des groupements plus ou moins ouverts, souvent rudélarisés (notamment *Tortuleto-Phleetum*). Nous ne l'avons jamais observée dans l'*A.-S.*, et Doing Kraft la trouva dans un seul *A.-S.*, un peu rudélarisé à Egmont. Ceci est très frappant: d'après le Prodrome, la présence de *Silene otites* est de 20–40 %, tandis qu'il apparait dans 70 % des relevés pris par de Leeuw dans l'*A.-S.* Par contre *Silene nutans* qui ne manque pratiquement dans aucun de nos relevés, a une présence de 40–60 % d'après le Prodrome, et de moins de 10 % chez de Leeuw. A notre avis, *Silene otites* ne peut être considéré comme caractéristique de l'*A.-S.* et il est donc recommandé de remplacer le nom de association à *Anthyllis maritima* et *Silene otites* (*Anthyllideto-Silenetum otites*) par: association à *Anthyllis maritima* et *Silene nutans* (*A.-S. nutantis*).

e. *Anthyllis vulneraria* et *Thalictrum minus* sont notés également dans l'association à *Anthyllis vulneraria* et *Trifolium scabrum.* Au cas où les mêmes sous-espèces se rencontreraient dans cette association, ce qui est très probable, ces espèces ne pourraient passer pour des caractéristiques locales de l'*A.-S.*, à moins de restreindre la notion de "local" au District des Dunes du Continent.

Peuvent également être considérées comme caractéristiques locales de l'*A.-S.* (local est considéré comme englobant les Districts de Wadden et des Dunes): *Erigeron acer*, *Picris hieracioides*, *Rhinanthus glaber* cf, *Silene nutans*, et pour la région entre Scheveningen et Katwijk, *Taraxacum commixtum.*

Le Tableau 1 comprend quelques relevés provenant de differentes régions de dunes. Les relevés sont conformes à la méthode de Braun–Blanquet (1928, 1951). Le Tableau III donne, pour les espèces principales, la présence et la valeur attribuée généralement à l'estimation combinée (quantité) dans les divers groupements

TABLEAU I

Anthyllideto-Silenetum de L. 1938

Sous-association	polypodietosum				sanguisorbetosum	cerastietosum
Variant à			Salix repens			
Numéro du relevé 1)	1	2	3	4	5	6
Auteur2), date, localité	DK 26.7.56 Egmond	Bb 26.7.56 Katwijk	DK 4.8.56 Noordwijkerh.	Bb 21.7.56 Wassenaar	DK 21.6.56 Bloemendaal	Bb 22.6.56 Katwijk
Surface en m^2	100	30	200	60	20	15
Exposition	N	N	N	N	NW	—
Inclinaison en °	30	15	30	20	20	—
Strate arbustive						
Hauteur en m			0.5	0.5	4.0	
Recouvrement en %			80	40	20	
Betula pendula Roth.					r.1	
Crataegus monogyna Jacq.				r.2	+.1	
Hippophae rhamnoides L.			r.1			
Ligustrum vulgare L.			+.3	1.3	+.3	
Quercus robur L.					r.1	
Salix repens L.			4.4	3.4		
Strate herbacée et muscinale						
Recouvrement en %	100	100	100	100	100	100
Caractéristiques locales de la ass.						
Arabis hirsuta (L.) Scop.			+.1		+.2	+.2
Botrychium lunaria (L.) Sw.					1.2	r.1
Carlina vulgaris L.	r.1		+.1	+.1	+.1	
Erigeron acer L.	+.2	+.1	r.1	+.1	+.2	+.1
Gentiana cruciata L.				1.2		
Picris hieracioides L.	1.2	+.2	+.1	2.2	+.2	
Rhinanthus glaber Lam.		2.1		2.1		+.1
Silene nutans L.	2.2	2.2		1.2		1.2
Taraxacum commixtum H.				+.1		
Caractéristiques d'unités supérieures						
Achillea millefolium L.	+.1	+.3				
Agrimonia eupatoria L.					r.1	
Anthyllis vulneraria L. ssp. maritima Schweigg.	2.2	+.1	+.2	+.2		2.2
Avena pubescens Huds.	+.1	2.1	1.2	2.1	1.3	1.2
Camptothecium lutescens (Huds.) B.S.		1.2				
Cerastium arvense L.	1.2		1.2		+.2	
Daucus carota L.	+.1	2.1	+.1	2.1		+.1
Euphrasia parviflora Schagerstr. var. glabrescens Wettst.				1.1		
Festuca ovina f. frisia A. et G.				1.3	3.3	
Galium verum L. var. maritimum D.C.				2.2	2.2	2.2
Hypnum cupressiforme L. var. elatum B.S.	4.4	4.5	1.2	3.4	2.3	5.5

TABLEAU I *(suite)*

Sous-association	polypodietosum				sanguisorbetosum	cerastietosum
Variant à			Salix repens			
Numéro du relevé ¹)	1	2	3	4	5	6
Auteur²), date, localité	DK 26.7.56 Egmond	Bb 26.7.56 Katwijk	DK 4.8.56 Noordwijkerh.	Bb 21.7.56 Wassenaar	DK 21.6.56 Bloemendaal	Bb 22.6.56 Katwijk
Knautia arvensis (L.) Coulter . . .	r.2					
Lotus corniculatus L. var. ciliatus Koch	1.2	2.2	+.2	2.2		+.3
Ononis repens L. var. mitis Spenn. .	+.2	1.3		1.2		
Orobanche vulgaris Poir.						+.1
Pimpinella saxifraga L.	+.1					
Plantago lanceolata L. var. sphaerostachya W. et Gr.	1.2	2.1		2.2		2.2
Poa pratensis L. var. humilis (Ehrh.) Gris..	2.2	2.1	2.2	2.3	2.2	+.2
Polygala vulgaris L. var. oxyptera Koch	+.1		+.2		+.2	1.3
Ranunculus bulbosus L.						2.2
Rhinanthus minor L.	1.2					
Thalictrum minus L. var. dunense Prod.				r.2		
Thymus serpyllum L. ssp. chamaedrys (Fr.) Vollm.	2.2	2.2	+.2	2.3	1.2	1.3
Espèces différentielles polypodietosum						
Brachythecium rutabulum (L.) B.S. .				+.2	1.2	
Didymodon rubellus (Hoffm.) B.S. .		+.2				
Fissidens adiantoides (L.) Hedw. . .				1.2		
Fragaria vesca L.			+.2			
Lophocolea bidentata (L.) Dum. . .		+.2		+.2		
Mnium affine Bland.				1.3	+.2	
Pleurozium schreberi Mitten			1.3			
Polygonatum odoratum (Mill.) Druce				+.2	r.1	
Polypodium vulgare L.	2.3	2.2	2.2	+.2		
Pyrola rotundifolia L.			2.1			
Rhytidiadelphus triquetrus (Hedw.) Warnst.	1.2		2.4			
Tortella flavovirens (Bruch) Broth. .		+.2		+.3		
Tortula subulata (L.) Hedw.		+.2		+.2		
Espèces différentielles sanguisorbetosum						
Rosa pimpinellifolia L.		+.2			2.2	1.2
Sanguisorba minor Scop.					2.2	
Veronica chamaedrys L.					1.2	
Viola hirta L.					+.1	
Espèces différentielles cerastietosum						
Cerastium semidecandrum L.. . . .	+.1					1.2
Sedum acre L.	1.2	+.1		+.2		1.2
Silene conica L.						+.2

TABLEAU I *(suite)*

Sous-association	polypodietosum				sangui-sorbe-tosum	ceras-tieto-sum
Variant à			Salix repens			
Numéro du relevé 1)	1	2	3	4	5	6
Auteur2), date, localité	DK 26.7.56 Egmond	Bb 26.7.56 Katwijk	DK 4.8.56 Noordwijkerh.	Bb 21.7.56 Wassenaar	DK 21.6.56 Bloemendaal	Bb 22.6.56 Katwijk
Autres espèces						
Ammophila arenaria (L.) Link	1.2	r.2				
Asparagus prostratus Richter				r.2		r.2
Bromus mollis L.		r.1				r.1
Bryum capillare L.		+.2		+.2		
Calamagrostis epogèios (L.) Roth	1.1		1.1	+.2	1.1	
Carex arenaria L.	+.1		+.1			
Cladonia furcata (Hds.) Schrad.		+.3				2.3
C. pyxidata (L.) Fr. var. chlorophaea (Flk.) Zopf.	+.2		+.2	+.2	+.2	
C. rangiformis Hffm.	1.3	2.3		1.2		
C. sylvatica (L.) Hffm.			+.2			+.2
Cochlearia danica L.	r.1					1.2
Dicranum scoparium (L.) Hedw.		+.2	2.3	+.3	2.3	
Festuca rubra L. subvar. arenaria (Osb.) Hack.	2.2	2.3	2.2	+.2	+.2	1.2
Galium mollugo L.	+.2	2.3	1.2	1.2		1.2
Hieracium pilosella L.	+.3	+.2		1.1		3.3
H. umbellatum L.	1.2	+.2	+.2			1.2
Hypochoeris radicata L.		+.1				r.1
Koeleria albescens D.C.	1.2	2.2		+.2		2.2
Luzula campestris (L.) D.C. ssp. vulgaris (Buch.) A. et G.	+.1	+.1	+.2	+.1	1.2	+.2
Pseudoscleropodium purum (L.) Limpr.	2.3		2.3		1.3	
Rubus caesius L.	+.2	4.3	2.2	2.2		2.2
Satureja acinos (L.) Scheele	+.2			+.2		
Taraxacum spec.	+.1	+.1	+.1	+.1	+.1	
Veronica officinalis L.				2.3	+.2	
Vicia lathyroides L.			+.2			+.2
Viola canina L.			+.1	+.2		

Relevé 1: Corynephorus canescens (L.) P.B. r. 2; Hippophae rhamnoides L. + .1; Peltigera canina (L.) Willd. + .2; Phleum arenarium L. + .1; Sagina nodosa (L.) Fenzl. r. 2; Silene otitis (L.) Wibel r. 1; Trifolium campestre Schreb. 1.2; Vicia hirsuta (L.) S. F. Gray + .2.

Rel. 2: Holcus lanatus L. r. 2.

Rel. 3: Asparagus officinalis L. r. 1; Hypnum cupressiforme L. var. ericetorum Br. eur. cf. 1.3.

Rel. 4: Agropyron repens (L.) P.B. r. 2; Cirsium vulgare (Savi) Ten. + .3; Linum catharticum L. + .2; Viola rupestris F. W. Schmidt + .2.

Rel. 5: Euonymus europaeus L. r. 1; Moehringia trinervia (L.) Clairv. r. 2; Myosotis collina Hoffm. + .1; Ranunculus acer L. r. 2; Saxifraga tridactylites L. + .1; Senecio jacobaea L. r. 1; Veronica arvensis L. + .1; Vicia angustifolia L. + .1.

reconnus. Dans la suite, nous reviendrons sur la classification donnée ici. Les relevés 1 à 4 (Tableau I) et les colonnes 8 à 11 (Tableau III) représentaient selon le Prodrome le stade optimum de l'*A.-S.* des pentes N. Les relevés 5 et 6 (Tableau I) et les colonnes 12 et 13 (Tableau III) représentent la forme sous laquelle se présente l'association sur terrain généralement plat.

L'*A.-S.* des pentes N possède plusieurs espèces différentielles par rapport à l'*A.-S.* des vallées. Un nombre remarquable de ces espèces se rencontrent dans le *Polypodieto-Empetretum*, l'association des pentes N du District de Wadden, tels *Polypodium vulgare*, *Veronica officinalis* et les Bryophytes *Hylocomium splendens*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus* et *Lophocolea bidentata*. D'autres espèces encore, qui sont notées régulièrement dans le *Polypodieto-Empetretum*, présentent ici une distribution optimum: *Hieracium umbellatum*, *Ammophila arenaria*, *Viola canina*, *Dicranum scoparium* et *Pseudoscleropodium purum*. La majorité de ces espèces colonise surtout les sols pauvres en carbonates, souvent un peu acides.

Il est remarquable de constater, que l'apparition de ce groupe d'espèces, va de pair avec l'augmentation du nombre des caractéristiques de l'association. Ces caractéristiques locales, considérées en gros, sont notées précisément dans les pelouses sèches, sur sol plus ou moins riche en carbonates. Dans cet exemple, les facteurs microclimatiques jouent pour le premier groupe d'espèces, un rôle plus important que les facteurs édaphiques.

Un troisième groupe d'espèces différencie encore les expositions N: ce sont les mousses *Didymodon rubellus*, *Encalypta contorta*, *Fissidens adiantoides*, *Tortula subulata*, et dans une moindre mesure *Ditrichum flexicaule* et *Tortella flavovirens*. Ces mousses recouvrent les parois presque verticales des terriers de lapin, ou des petits affaisements à l'exposition N, mais se trouvent aussi plus ou moins régulièrement dans l'*A.-S.* voisin.

Enfin, au sein de l'*A.-S.*, *Polygonatum odoratum* et *Pyrola rotundifolia* sont manifestement liés aux pentes N, tandis que *Antennaria dioica*, *Fragaria vesca*, *Cerastium triviale*, *Eurynchium striatum* et *Brachythecium rutabulum* manifestent également une préférence pour cette station.

Les différences au sein de l'*A.-S.*, entre pentes N et terrain plat, apparaissent le plus clairement en comparant les colonnes 9 et 13 (Tableau III), basées sur des relevés provenant de la région située au N de Katwijk, où l'*A.-S.* est le mieux développé. Pour les pentes N,

Rel. 6: Bryum spec. + .2; Ceratodon purpureus (L.) Brid. + .2; Cornicularia aculeata (Schreb.) Th. Fr. + .2.

[1] Les analyses pédologiques des numéros 2 et 4 ont donné les résultats suivants: Horizon Al (respectivement): limite inférieure 6 cm et 10 cm; pH H_2O 7, 4 et 7,3; pH KCl 7,1 et 7,1; $CaCO_3$ v-% 1,7 et 1,1; humus-% 3,4 et 3,2; N total-% 0,11 et 0,10; P total-% 0,04 et 0,04.

Horizon A_2 (resp.): limite inférieure 25 cm et 25 cm; pH H_2O 8,1 et 8,3; pH KCl 7,6 et 7,7; $CaCO_3$-% 2,9 et 2,9; humus-% 1,0 et 0,7; N total-% 0,03 et 0,02; P total-% 0,03 et 0,03.

[2] DK = H. Doing Kraft, Bb = J. H. A. Boerboom.

plusieurs espèces sont des différentielles absolues. Des espèces, renseignées jusque dans la colonne 13, mais totalement absentes des pentes N, n'existent pas. Par contre, il est manifeste que quelques espèces sont nettement mieux représentées dans le groupement des terrains plats. En premier lieu il s'agit d'espèces de stations bien ensoleillées: *Achillea millefolium*, *Cerastium arvense*, *Galium verum* et *Hieracium pilosella*. Ensuite nous notons des espèces qui présentent en général une préférence pour les types de végétation ouverts: *Arenaria serpyllifolia*, *Cerastium semidecandrum*, *Cochlearia danica*, *Koeleria albescens*, *Sedum acre* et *Silene conica*. Ainsi apparaissent des liens de ressemblance aussi bien avec le *Tortuleto-Phleetum* qu'avec le *Taraxaco-Galietum* (voir Ch. 3).

Les pentes des dunes à roses (*Rosa pimpinellifolia*) de Bloemendaal relèvent en partie de l'*A.-S.*, vu la présence de *Arabis hirsuta*, *Picris hieracioides*, *Silene nutans*, etc. Certaines espèces "significatives" semblent cependant manquer, comme *Anthyllis vulneraria*, *Daucus carota* et *Pimpinella saxifraga*. D'autre part, *Sanguisorba minor*, manquant ailleurs dans les dunes néerlandaises, est ici très abondant; *Viola hirta* et *Veronica chamaedrys* sont plus communs ici qu'autre part dans l'*A.-S.* La présence d'*Evonymus europaeus* dans la plupart des relevés pris dans cette région, s'explique par la constance de cet arbuste dans les dunes des environs de Haarlem. Au sein de l'association, les différences phytosociologiques entre versants exposés au N et terrains plats, sont moins marquées que dans les autres régions. Dans son ensemble cependant, la végétation s'écarte notablement de l'*A.-S.* de Katwijk.

On peut établir une subdivision de l'association en trois types, ayant rang de sous-association, et nommés de la manière suivante: sur les versants exposés au N (Tableau I, colonnes 1 à 4; Tableau III, colonnes 8 à 11) l'*A.-S. polypodietosum*, sur terrain généralement plat dans la région de Katwijk (Tableau I, colonne 6; Tableau III, colonne 13) l'*A.-S. cerastietosum semidecandrae* et sur même terrain près de Bloemendaal (Tableau I, colonne 5; Tableau III, colonne 12) l'*A.-S. sanguisorbetosum*.

On peut distinguer dans l'*A.-S. polypodietosum*, une variante où *Salix repens* domine (Tableau III, colonne 10 et 11). On y trouve très souvent *Pyrola rotundifolia*, qui dans la région des dunes, semble lié presque exclusivement à *Salix repens*. Dans cette variante à *Salix repens*, les caractéristiques de l'association et des unités supérieures, sont en général moins bien représentées que dans la variante sans *Salix repens*. Si ces espèces reculent encore plus, cette végétation ne relèvera plus de l'*A.*-S., mais bien de la sociation à *Salix repens*, éventuellement d'une association encore à décrire (affinités avec l'association à *Salix repens* et *Thalictrum minus* Tx. 1937 et le *Polypodieto-Salicetum arenariae*, cfr. Tuexen, 1956).

L'apparition plus fréquente d'autres plantes ligneuses (*Crataegus monogyna*, *Ligustrum vulgare*, *Quercus robur*) signale une tendance à la succession vers le hallier (*Prunetalia spinosae*).

Cette variante à *Salix repens* est caractérisée dans la région des dunes entre Scheveningen et le Wassenaarse Slag, par la présence très cummune de *Gentiana cruciata* et une grande richesse floristique, très grande même pour l'*A.-S.*: on pourrait parler ici d'une sous-variante à *Gentiana cruciata*. Ailleurs on pourrait également distinguer des sous-variantes, en relation avec l'apparition très locale de quelques espèces (une sous-variante à *Satureja vulgaris* à Noordwijkerhout, à *Knautia arvensis* près d'Egmont).

3. LE TARAXACO-GALIETUM MARITIMI (ass. nov.)

Plusieurs phytosociologues néerlandais inclinent à penser, que les pelouses fermées des pannes sèches du District des Dunes, relèvent en ordre principal du *Festuceto-Galietum*, décrit d'Ameland.

En ce cas, nous aurions à faire ici à la sous-association à *Koeleria albescens*, décrit de Texel par WESTHOFF (1946) (cfr. HOFFMANN et WESTHOFF, 1951). DE LEEUW (1938) cite le *F.-G.* seulement pour le District de Wadden et l'ancien paysage des dunes, entre autres de Noordwijkerhout.

A notre avis, le *F.-G.* existe bien dans le District des Dunes, mais n'y joue qu'un rôle effacé, quant à la surface occupée.

Nous avons déjà dit que les groupements herbeux des zones peu déclives des dunes entre Katwijk et Noordwijk et de Bloemendaal, relèvent de l'*A.-S.* sur base de la composition floristique. Ailleurs également on note des groupements affines de l'*A.-S.*, ou relevant même de cette association. Mais à côté de ces types, on rencontre des groupements dans lesquels les caractéristiques de l'*A.-S.* ne jouent qu'un rôle très subordonné quant au recouvrement et à l'abondance, cependant qu'un grand nombre de caractéristiques du *F.-G.* font défauts.

Ainsi, dans les vallées des dunes entre Scheveningen et le Wassenaarse slag domine un groupement végétal, qui à part la présence de quelques espèces communes des pelouses sèches, est caractérisé par:

a. une dominance presque générale de *Festuca ovina*.
b. le rôle important de plusieurs espèces, répandues également dans l'*A.-S.* comme *Avena pubescens*, *Ononis repens* var. *mitis*, *Thymus serpyllum* ssp. *chamaedrys*, *Polygala vulgaris* var. *oxyptera*.
c. l'abondance particulière de plusieurs espèces de *Taraxacum*: *Taraxacum taeniatum* H., *T. agaurum* v. Soest, *T. rubicundum* Dt., *T. laetiforme* Dt., *T. dunense* v. Soest et *T. obliquum* Fr.
d. une présence élevée de *Viola rupestris*.

Le Tableau II et le Tableau III, colonnes 6 et 7, se rapportent à ce groupement. Quoique ce type représente, sous certains aspects, un état intermédiaire entre le *Festuceto- Galietum* et l'*Anthyllideto-Silenetum*, il nous semble par ailleurs qu'il possède à suffisance un caractère original pour mériter le rang d'association indépendante. Le nom choisi pour le groupement, *Taraxaco-Galietum* (indiqué sous les initiales de *T.-G.*) est justifié par l'abondance des espèces de *Taraxacum* dans l'association. Notre connaissance de l'affinité sociologique des espèces de *Taraxacum* est cependant encore fragmentaire, et une étude intensive à ce sujet n'a pu être réalisée que dans les dunes entre Scheveningen et Katwijk. En conséquence, nous ne pouvons encore certifier quelles

TABLEAU II[1])

Taraxaco-Galietum maritimi ass. nov.

Sous-association	cladonietosum			plantaginetosum		
Numéro du relevé	1	2	3	4	5	6
Date	13.5.56	25.6.56	15.6.56	22.5.56	14.5.56	25.7.56
Surface en m²	5	4	8	8	4	8
Exposition	E	—	—	N	—	—
Inclinaison en °	5	—	—	5	—	—
Horizon A1						
Couche analysée en cm		1–9[2])	0–10		3–7	0–9
pH H_2O		7.0	6.8		7.7	7.6
pH KCl		6.5	6.3		6.9	7.3
$CaCO_3$-%		0.3	0.2		1.5	1.3
Humus-%		5.4	2.7		2.6	3.8
N total-%		0.19	0.09		0.10	0.15
N total/humus × 100		3.4	3.3		3.8	4.0
P total-%		0.03	0.03		0.03	0.04
Horizon A2						
Couche analysée en cm		15–20	10–23		15–20	9–20
pH H_2O		7.5	7.7		7.7	8.1
pH KCl		7.3	7.1		7.1	7.6
$CaCO_3$-%		2.7	0.9		2.7	3.6
humus-%		0.4	1.4		0.8	1.3
N total-%		0.01	0.05		0.03	0.04
N total/humus × 100		2.5	3.6		3.7	3.1
P total-%		0.02	0.03		0.02	0.03
Strate herbacée et muscinale						
Recouvrement en %	100	100	100	100	100	100
Caractéristiques locales de la association						
Carex flacca Schreb.					+.1	+.1
Taraxacum obliquum Fr.	+.1	+.1	+.1	+.1	1.1	r.1
Viola rupestris F. W. Schmidt		+.2		+.2	+.2	+.2
Caractéristiques d'unités supérieures						
Avena pubescens Huds.	1.1	2.2	2.1	2.2	2.1	2.1
Camptothecium lutescens (Huds.) Br. eur.				+.2		r.1
Carex arenaria L.	1.1		1.1			+.2
Cerastium arvense L.	1.2		1.1			1.1
Euphrasia parviflora Schagerstr. var. glabrescens Wettst.		+.1			1.1[3])	+.1
Festuca ovina f. frisia A. et G.	3.2	3.2	3.2	2.2	3.4	2.2
Galium verum L. var. maritimum D.C.	2.1	2.2	2.1	2.1	2.1	2.1
Hypnum cupressiforme L. var. elatum B. et S.	2.3	3.4	5.5	5.5	4.5	3.3
Koeleria albescens D.C.	+.2	1.2	2.2	+.2	2.2	2.2
Lotus corniculatus L. var. ciliatus Koch cf.	1.2	1.2	1.2	2.2	2.2	2.3
Ononis repens L. var. mitis Spenn	1.1	+.2		+.1	2.1	2.4
Orobanche vulgaris Poir			+.1			r.1
Poa pratensis L. var. humilis (Ehrh.) Gris.		1.2	+.1			+.1

TABLEAU II *(suite)*

Sous-association	cladonietosum			plantaginetosum		
Numéro du relevé	1	2	3	4	5	6
Date	13.5.56	25.6.56	15.6.56	22.5.56	14.5.56	25.7.56
Polygala vulgaris L. var. oxyptera Koch			+.2	+.2	+.1	+.2
Satureja acinos (L.) Scheele		r.2		+.1	+.1	+.2
Sedum acre L.		+.2		+.2	1.1	+.2
Senecio jacobaea L. var. flosculosus Lam. et D.C.	+.2		+.2	1.1	+.1	+.1
Taraxacum agaurum v. S.			+.1	r.1		
T. brachyglossum Dt.						+.1
T. rubicundum Dt.				+.1	+.1	+.1
T. taeniatum H.		+.1	+.1	+.1	+.1	
Thymus serpyllum L. ssp. chamaedrys (Fr.) Vollm.			+.3	+.2	+.2	3.3
Espèces différentielles cladonietosum						
Cladonia foliacea (Hds.) Schaer. var. alcicornis (Lght.) Schaer.	+.2	+.2				
C. pyxidata (L.) Fr. var. chlorophaea (Flk.) Zopf.	+.2	+.2				
C. sylvatica (L.) Hffm.	3.3		3.3			
Hypochoeris radicata L.		r.1				
Rumex acetosella L.	+.1	r.1				
Espèces différentielles plantaginetosum						
Achillea millefolium L.						2.1
Arabis hirsuta (L.) Scop.				r.2		+.2
Linum catharticum L.					+.1[3]	2.1
Plantago lanceolata L. var. sphaerostachya W. et Gr.				2.1	1.2	2.1
Silene nutans L.		r.2		+.2		r.2
Autres espèces						
Bryum sp.					+.2	+.2
Calamagrostis epigeios (L.) Roth	2.2	+.1	1.1	1.1	1.1	2.2
Carlina vulgaris L.		r.1				r.1
Cladonia furcata (Hds.) Schrad.	+.2		+.2			+.2
C. rangiformis Hffm.		3.4		1.2		3.3
Crataegus monogyna Jacq.	+.1					r.1
Ditrichum flexicaule (Schleich.) Hampe var. densum B. et S.				+.2	+.2	
Galium mollugo L.	+.1	+.2				+.3
Hieracium pilosella L.	2.3	2.1	2.3	1.1	+.2	1.2
Luzula campestris (L.) D.C. ssp. vulgaris (Buch.) A. et Gr.	1.1	+.2	2.2	2.1	+.2	+.1
Rubus caesius L.		+.2		1.2	+.2	r.1
Taraxacum sp.			+.1		+.1	1.1
Veronica officinalis L.			r.1		+.1	

Relevé 1: Dicranum scoparium (L.) Hedw. 1.2;
Rel. 3: Leontodon nudicaulis (L.) Banks et Lowe + .2; Pseudocleropodium purum Limpr. +.3; Taraxacum tortilobum Flor. r. 1; Vicia lathyroides L. + .2;
Rel. 6: Asparagus prostratus Richter r. 2; Erigeron acer L. + .1; Gentiana

espèces de *Taraxacum* sont de fait des caractéristiques de la nouvelle association. Il est clair cependant, que la plupart des *Taraxaca* se rencontrent également dans l'*A.-S. polypodietosum*, quoique en quantité plus faible. *Taraxacum obliquum* montre un optimum très net pour le *T.-G.* dans la région au N de Scheveningen, de sorte que nous pouvons provisoirement considérer l'espèce comme caractéristique.

Ainsi que nous l'avons déjà dit dans le chapitre précédent, *Viola rupestris* montre également une préférence pour ce groupement; de plus *Carex flacca* peut aussi être considéré comme une caractéristique locale du *T.-G.*

Le *Taraxaco-Galietum* comprend deux sous-associations, nommées comme suit: *T.-G. plantaginetosum* et *T.-G. cladonietosum.*

Le *T.-G.plantaginetosum* se distingue de l'autre sous-association, par la présence plus ou moins régulière de quelques espèces ayant leur distribution principale dans l'*A.-S.* Le groupement est quelque peu plus herbeux. A côté de *Plantago lanceolata var. sphaerostycha*, les espèces différentielles sont *Achillea millefolium, Arabis hirsuta et Linum catharticum.*

Dans le *T.-G. cladonietosum* par contre, on note quelques espèces qui, dans la même région, jouent un rôle important dans le *Violeto-Corynephoretum*, tandis que la ressemblance avec le *F.-G.* augmente. Des espèces comme *Corynephorus canescens*, *Hieracium umbellatum*, *Hypochoeris radicata*, *Leontodon nudicaulis*, *Rumex acetosella*, *Veronica officinalis* et *Viola canina* sont, il est vrai, peu communes, et faiblement associées entre elles, mais elles indiquent une tendance dans cette direction. Le fait également, que *Carex arenaria*, *Hieracium pilosella* et *Luzula campestris* apparaissent plus souvent, ou avec un recouvrement plus important, est significatif. Les espèces différentielles sont à rechercher dans le premier groupe, à côté desquelles il convient de citer *Cladonia foliacea*, *C. pyxidata*, *C. silvatica* et *Cornicularia aculeata.*

Localement, le *T.-G.* se présente sous un facies à *Calamagrostis epigeios*. En ce cas, la grande richesse floristique de l'association diminue quelque peu, cependant qu'on note un recul plus important de l'abondance et de la vitalité de plusieurs espèces.

Le *T.-G.* peut succéder au *Tortuleto-Phleetum.* Il n'est pas exclu que le lapin ait contribué au maintien de l'association. Lorsque *Salix repens* parvient à s'installer dans le gazon, la vitalité de *Festuca ovina* diminue; par contre, quelques espèces de l'*A.-S.* deviennent alors plus abondantes: *Picris hieracioides*, *Daucus carota*, *Gentiana cruciata.* Ainsi apparaissent de multiples stades de transition entre le *T.-G.*, l'*A.-S.* et la sociation à *Salix repens* (cf. association à *Salix repens*).

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cruciata L. (r. 2); Ligustrum vulgare L. (r. 2); Lophocolea bidentata (L.) Dum. + .2; Mnium affine Blandow 1.2; Picris hieracioides L. + .2; Tortella flavovirens (Bruch) Broth. + .2.

[1] Tous les relevés proviennent de Wassenaar.

[2] Moyennes de 2 analyses (1–4 et 6–9 cm). Les chiffres de détail furent respectivement: pH H_2O 6.8 et 7,1; pH KCl 6,2 et 6,8; $CaCO_3$-% 0,0 et 0,5; humus-% 9,5 et 1,3; N total-% 0,34 et 0,04; N total/humus × 100 3,6 et 3,1; P total-% 0,04 et 0,01.

[3] Noté le 15 juillet 1956.

4. COMPARAISON ENTRE CERTAINES PELOUSES FERMÉES DE LA CÔTE DE LA MER DU NORD ET DISCUSSION SUR LEUR POSITION SYSTÉMATIQUE

Le Tableau III réunit tous les relevés disponibles des pelouses sèches et fermées des côtes néerlandaise, belge en française et qui ont de l'importance pour nos considérations; les colonnes 1, 4 et 14 comportent les relevés déjà publiés, les autres colonnes les relevés inédits.

Les espèces sont ventilées dans les groupes suivants:

1. espèces reparties plus ou moins régulièrement dans les associations considérées, et qui sont caractéristiques des pelouses sèches en général.
2. espèces absentes du *F.-G.*, mais présentes dans les autres associations.
3. espèces communes à l'*A.-S.* et à l'association à *Anthyllis vulneraria* et *Trifolium scabrum*, et qui manquent dans le *F.-G.* et le *T.-G.*
4. espèces présentant, au sein des groupements étudiés, un optimum de distribution dans le *F.-G.*, mais qui apparaissent régulièrement, en partie, dans l'association à *Anthy. v.* et *Trif. sc.*
5. caractéristiques locales du *F.-G.*
6. caractéristiques locales du *T.-G.*
7. caractéristiques locales de l'*A.-S.*
8. caractéristiques locales de l'ass. à *Anthy. v.* et *Trif. sc.*
9. principales espèces différentielles, pour autant qu'elles ne soient pas mentionnées plus haut.
10. autres espèces principales.
11. espèces peu représentées, ou qui sont peu importantes sous le rapport de la typification ou de la différentiation des associations; ces espèces ne sont pas reprises dans le bloc-diagramme.

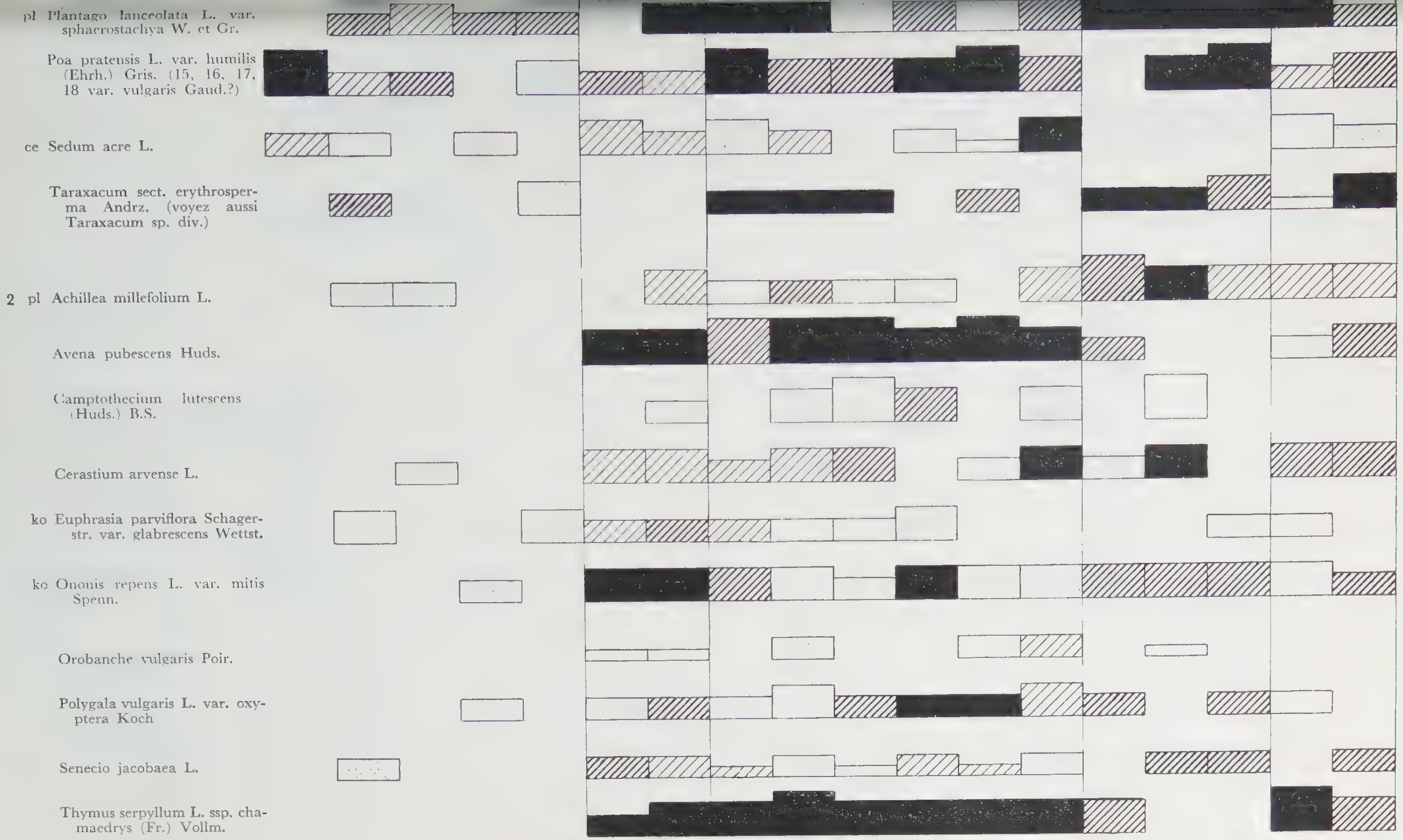
L'*Anthyllideto-Silenetum* et le *Taraxaco-Galietum* ayant déjà été discutés en détail et leurs particularités ressortant suffisamment du tableau, nous nous limiterons surtout à quelques remarques concernant les relations réciproques des associations. La place centrale dans le Tableau III, revient à l'*A.-S.* Cette association montre des affinités, aussi bien avec le *F.-G.* (un grand nombre de plantes des dunes en commun, espèces du Koelerion), qu'avec l'association à *Anthyllis vulneraria* et *Trifolium scabrum* (espèces fluviatiles, avec souvent un penchant vers le *Bromion*). Cette dernière association surtout, est très riche en espèces fluviatiles, et présente de ce fait une très grande communauté avec l'association affine du *Medicagineto-Avenetum pubescentis* de L. 1937, un groupement prairial des digues riches en calcaire, le long des grandes rivières. Sont particulièrement caractéristiques de l'ass. à *Anthy. v.* et *Trif. sc.*, les multiples (9) et souvent intéressantes espèces de trêfle: *Trifolium filiformis*, *T. scabrum*, *T. striatum*, *T. subterraneum*. Le caractère prairial de ce groupement, est souligné par la haute présence de *Trifolium repens*, *Convolvulus arvensis* et parfois de *Bellis perennis*. Il est remarquable de constater, que quelques espèces, ordinairement indicatrices de sols pauvres en carbonates de Ca, se rencontrent régulièrement dans le groupement: *Hypochoeris radicata*,

(suite p. 668)

TABLEAU III

Comparaison de la composition floristique entre un certain nombre de pelouses sèches des côtes néerlandaise, belge et française septentrionale

groupes (voyez texte)	espèce différentielle ¹)	colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
		sous-association	agrostidetosum				koele-rietosum	cladonie-tosum	plantagi-netosum	polypodietosum				sangui-sorbe-tosum	cerastie-tosum					
		localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijker-hout (Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK et Bb)	Wassenaar (Bb.)	Bloemendaal (DK.)	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
		nombre de relevés considérés	2	10	4	6	7	7	12	6	8	10	14	6	9	3	10	4	15	9
1		Bromus mollis L. var. nanus (Weig.) A. et G.			⬚				□	□	⬚	□	□	□	▨		▨	▨		
		Carex arenaria L.	■	▨	■	■	■	■	▨	■	▨	⬚	⬚	□	▨	▨	■	■	■	▨
	ce	Cerastium semidecandrum L.	■	▨			▨	▨	□	▨	□	▨			■		■	■	□	▨
		Festuca ovina L. f. frisia A. et G.	■	■	■	▨	■	■	■	■	□	□	■	■	□			⬚	■	□
		Festuca rubra L. subvar. arenaria (Osb.) Hack.	▨	▨		■	▨			■	■	▨	■	▨	■		□		■	■
		Galium verum L. var. maritimum D.C.	■	■		■	■	■	■	■	▨	▨	■	■	■	■	■	■	■	■
		Hieracium pilosella L.		□	■	■	■	■	■	■	■	▨	■	▨	■	■	▨	■	▨	▨
		Lotus corniculatus ssp. eu-corniculatus A. et G. (6–14, 17 var. ciliatus Koch cf.)	▨	▨	▨	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▨



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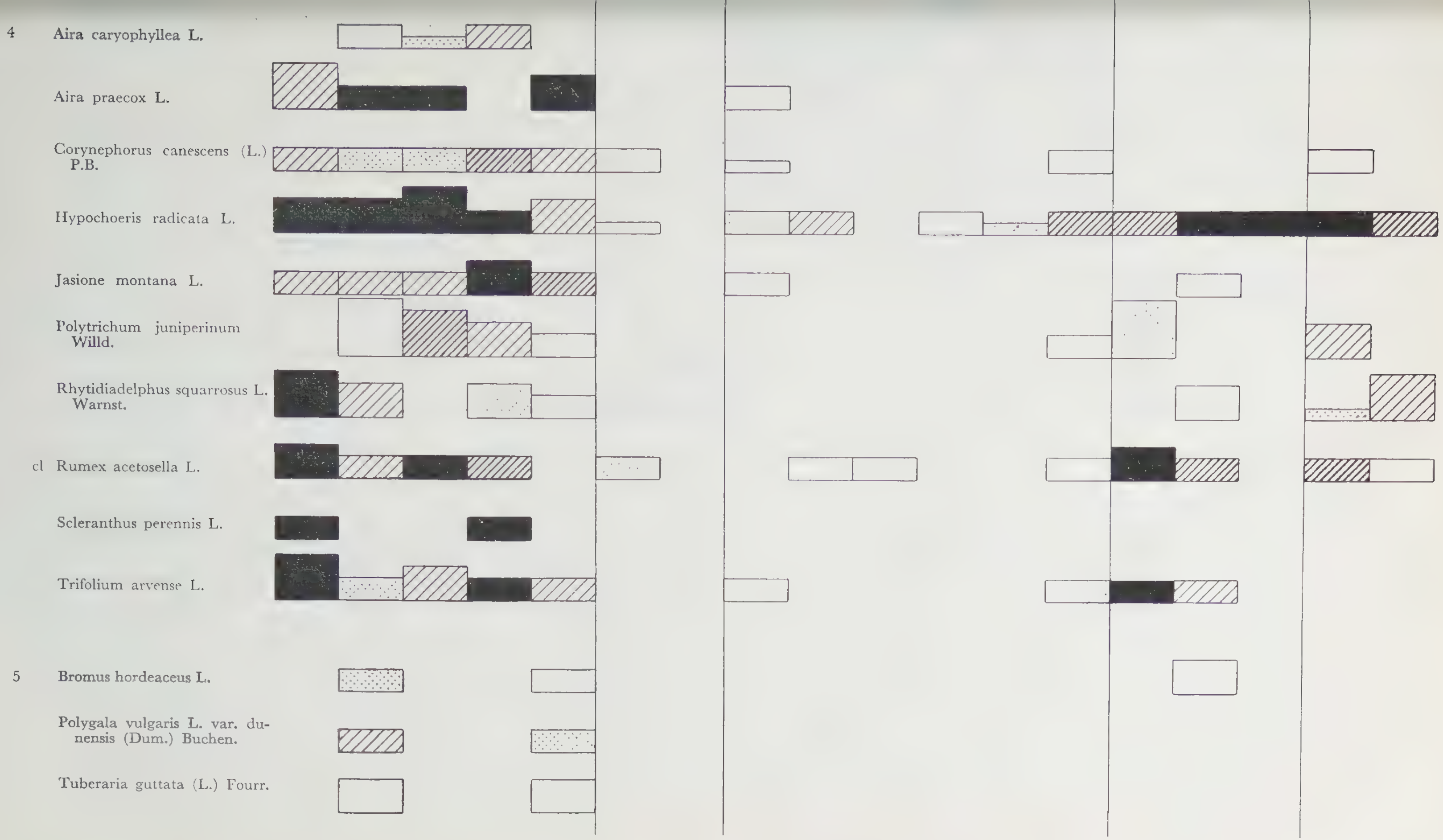
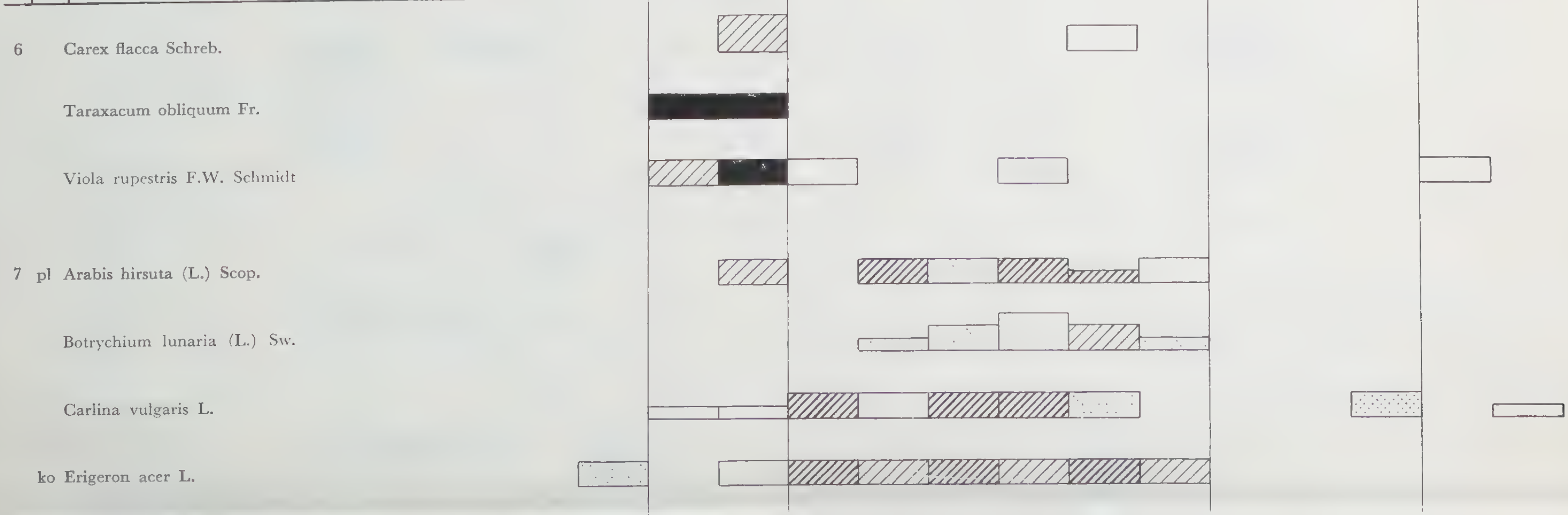
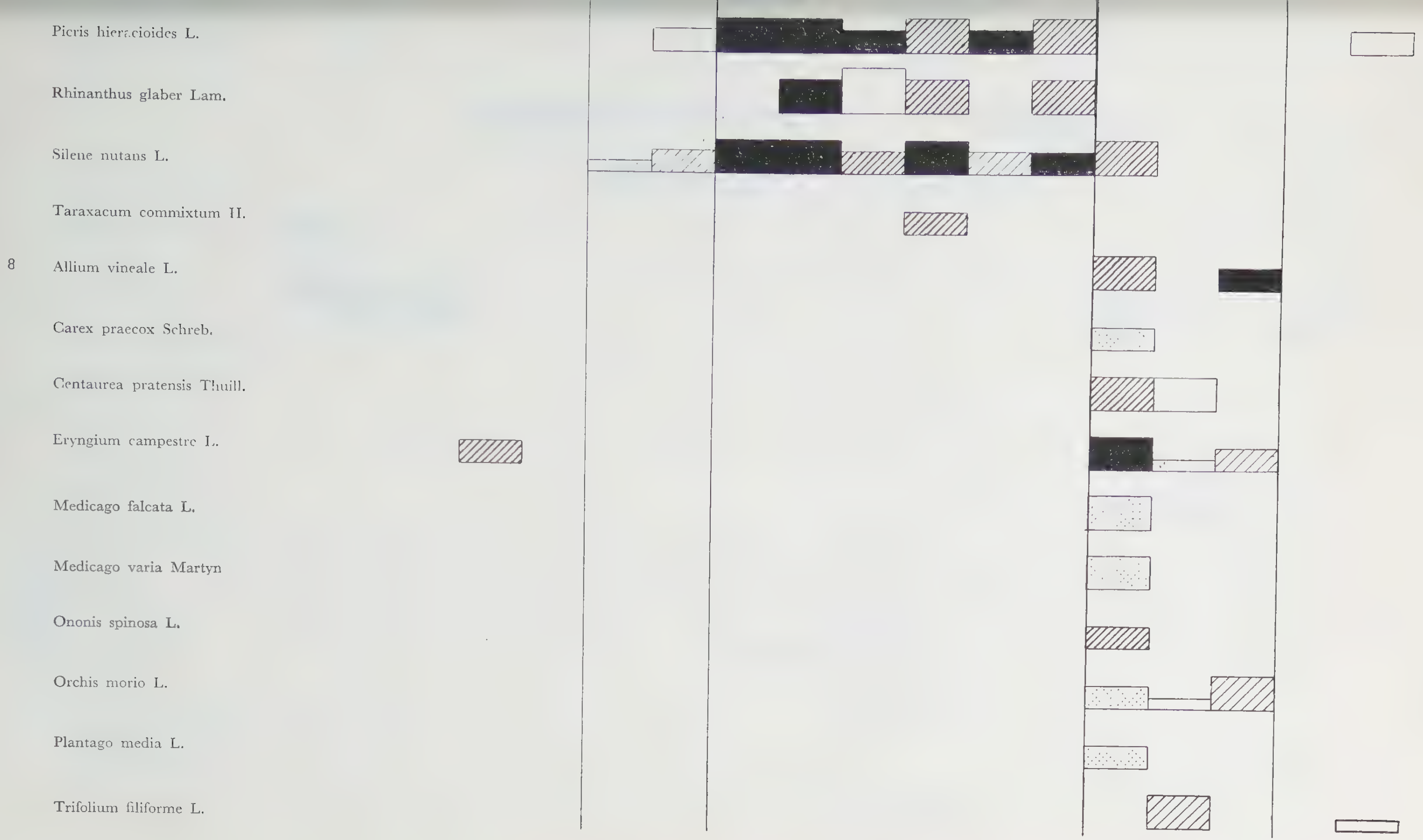
1) ag = F.-G. agrostidetosum; ce = A.-S. cerastietosum; cl = T.-G. cladonietosum; ko = F.-G. koelerietosum; pl = T.-G. plantaginetosum; po = A.-S. polypodietosum; sa = A.-S. sanguisorbetosum.

groupes (voyez texte)	espèce différentielle ¹)	colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
		sous-association	agrostidetosum				koelerietosum	cladonietosum	plantaginetosum	polypodietosum				sanguisorbetosum	cerastietosum					
		localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijkerhout (Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK.)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK. et Bb.)	Wassenaar (Bb.)	Bloemendaal (DK.)	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
		nombre de relevés considérés	2	10	4	6	7	7	[illegible]	6	8	10	14	6	9	3	10	4	15	9
3		Agrimonia eupatoria L.								☐		░	☐	░		▨				
		Anthyllis vulneraria L. (8–12, 13 ssp. maritima Schweigg.)								░	■	░	▨		■	■	☐			
		Daucus carota L.								▨	■	▨	▨		▨	■				
		Knautia arvensis (L.) Coulter								░		☐				■				
		Pastinaca sativa L.										☐		☐						
		Pimpinella saxifraga L.								▨	▨	░			▨	░				☐
		Ranunculus bulbosus L.			☐						▨	▨		░	░	■	■	■	░	▨
	sa	Sanguisorba minor Scop.												■						

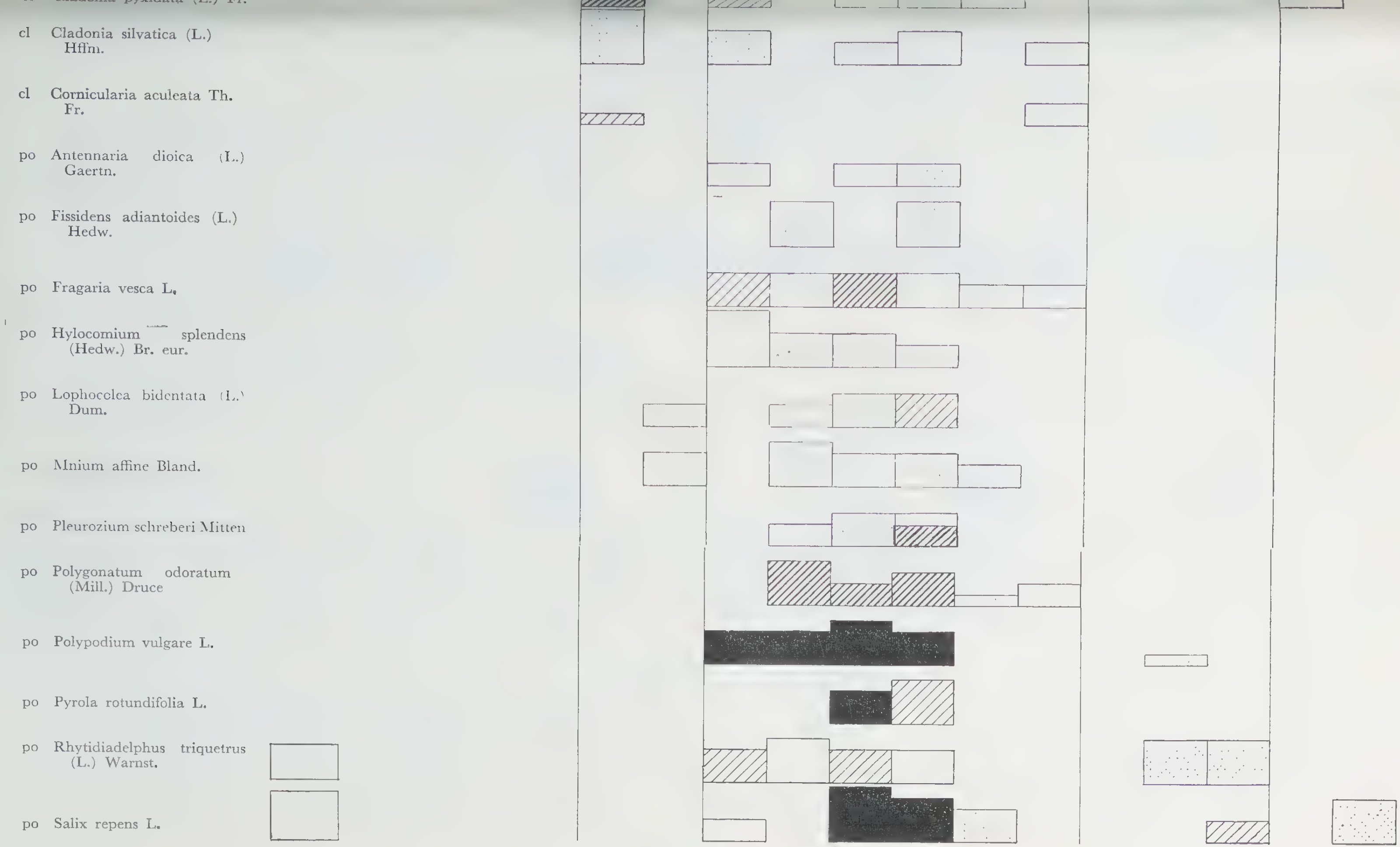

4
Aira caryophyllea L.
Aira praecox L.
Corynephorus canescens (L.) P.B.
Hypochoeris radicata L.
Jasione montana L.
Polytrichum juniperinum Willd.
Rhytidiadelphus squarrosus L. Warnst.
cl
Rumex acetosella L.
Scleranthus perennis L.
Trifolium arvense L.
5
Bromus hordeaceus L.
Polygala vulgaris L. var. dunensis (Dum.) Buchen.
Tuberaria guttata (L.) Fourr.

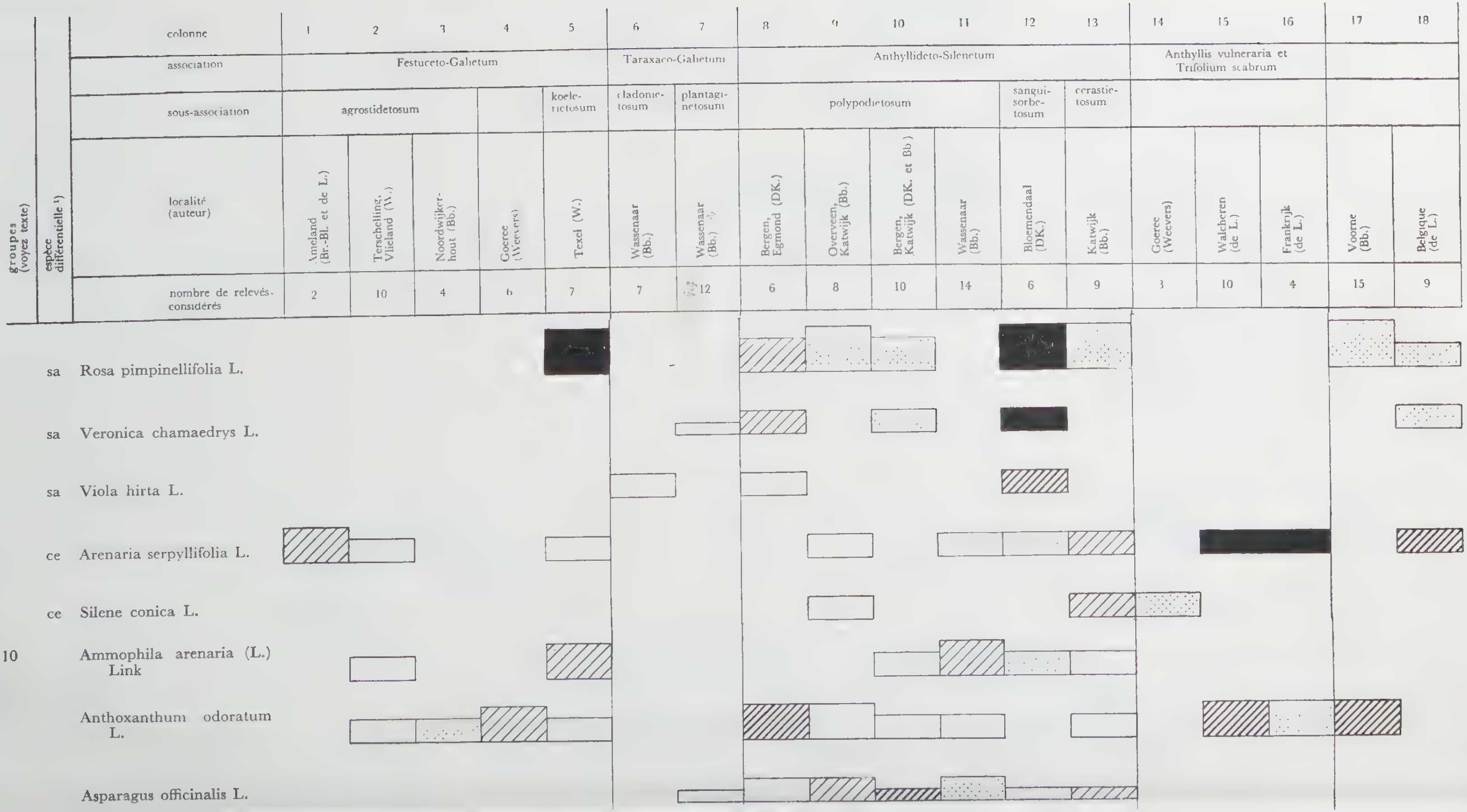
groupes (voyez texte)	espèce différentielle 1)																			
		colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
		sous-association	agrostidetosum				koelerietosum	cladonietosum	plantaginetosum	polypodietosum				sanguisorbetosum	cerastietosum					
		localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijkerhout (Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK.)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK. et Bb.)	Wassenaar (Bb.)	Bloemendaal (DK.)	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
		nombre de relevés considérés	2	10	4	6	7	7	12	6	8	10	14	6	9	3	10	4	15	9



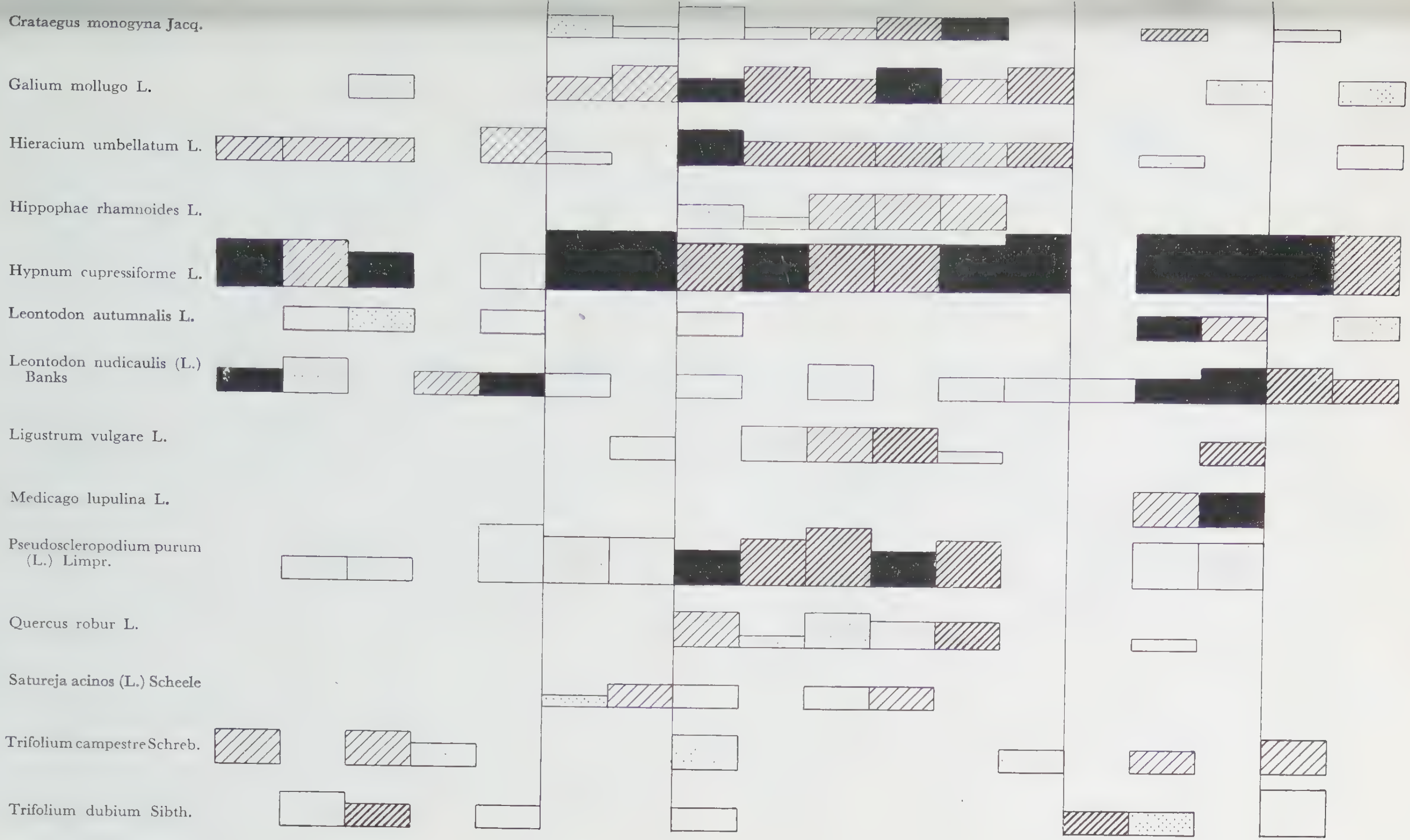

Picris hieracioides L.
Rhinanthus glaber Lam.
Silene nutans L.
Taraxacum commixtum H.
8
Allium vineale L.
Carex praecox Schreb.
Centaurea pratensis Thuill.
Eryngium campestre L.
Medicago falcata L.
Medicago varia Martyn
Ononis spinosa L.
Orchis morio L.
Plantago media L.
Trifolium filiforme L.

groupes (voyez texte)	espèce différentielle ¹)	colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
		sous-association	agrostidetosum				koele-rietosum	cladonie-tosum	plantagi-netosum	polypodietosum				sangui-sorbe-tosum	cerastie-tosum					
		localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijker-hout Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK.)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK. et Bb.)	Wassenaar Bb.)	Bloemendaal (DK.)	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
		nombre de relevés considérés	2	10	4	6	7	7	12	6	8	10	14	6	9	3	10	4	15	9
		Trifolium scabrum L.														▨	■	▨		□
		Trifolium striatum L.														▨	▨	▨		
		Trifolium subterraneum L.															▨			
9	ag	Agrostis tenuis Sibth.	■	■	■	▨				□				□		■	░		■	▨
	ag	Peltigera sp.	■	▨			□		░	░							░	▨	□	░
	ko	Calamagrostis epigeios (L.) Roth					▨	■	■	■	▨	▨	■	■	▨				░	
	ko	Koeleria albescens DC.		□		■	■	■	■	■	■	░	■	■	■	▨		░		▨
	ko	Linum catharticum L.		□			░		▨	□	░	□	▨		□			▨		


cl Cladonia silvatica (L.) Hffm.
cl Cornicularia aculeata Th. Fr.
po Antennaria dioica (L.) Gaertn.
po Fissidens adiantoides (L.) Hedw.
po Fragaria vesca L.
po Hylocomium splendens (Hedw.) Br. eur.
po Lophocolea bidentata (L.) Dum.
po Mnium affine Bland.
po Pleurozium schreberi Mitten
po Polygonatum odoratum (Mill.) Druce
po Polypodium vulgare L.
po Pyrola rotundifolia L.
po Rhytidiadelphus triquetrus (L.) Warnst.
po Salix repens L.



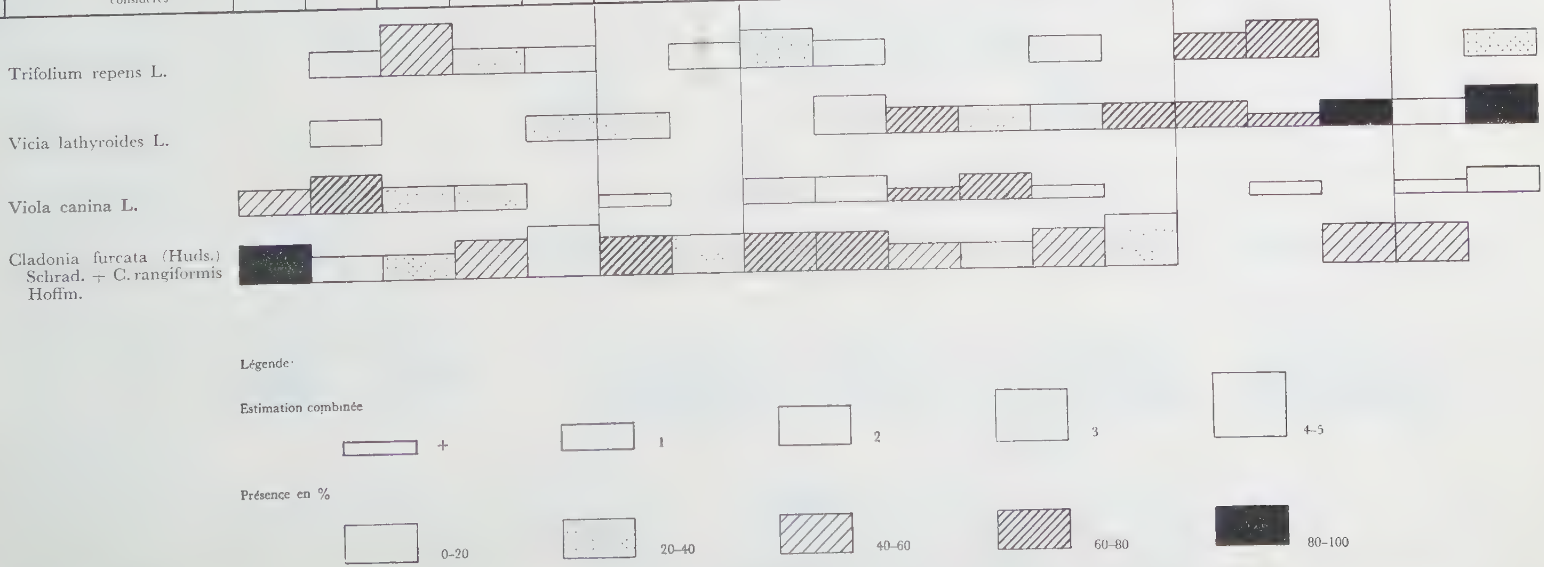
groupes (voyez texte)	espèce différentielle ¹)	colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
		sous-association	agrostidetosum				koele-rietosum	cladonie-tosum	plantagi-netosum	polypodietosum				sangui-sorbe-tosum	cerastie-tosum					
		localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijker-hout (Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK.)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK. et Bb.)	Wassenaar (Bb.)	Bloemendaal (DK.)	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
		nombre de relevés considérés	2	10	4	6	7	7	12	6	8	10	14	6	9	3	10	4	15	9
	sa	Rosa pimpinellifolia L.					■			▨	░	░		■	░				░	░
	sa	Veronica chamaedrys L.							□	▨		░		■						░
	sa	Viola hirta L.						□		□				▨						
	ce	Arenaria serpyllifolia L.	▨	□			□				□		□	□	▨		■	■		▨
	ce	Silene conica L.									□				▨	░				
10		Ammophila arenaria (L.) Link		□			▨					□	▨	░	□					
		Anthoxanthum odoratum L.		□	░	▨	□			▨	□	□	□		□		▨	░	▨	
		Asparagus officinalis L.							□	□	▨	▨	░	□	▨					


Crataegus monogyna Jacq.
Galium mollugo L.
Hieracium umbellatum L.
Hippophae rhamnoides L.
Hypnum cupressiforme L.
Leontodon autumnalis L.
Leontodon nudicaulis (L.) Banks
Ligustrum vulgare L.
Medicago lupulina L.
Pseudoscleropodium purum (L.) Limpr.
Quercus robur L.
Satureja acinos (L.) Scheele
Trifolium campestre Schreb.
Trifolium dubium Sibth.

colonne	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
association	Festuceto-Galietum					Taraxaco-Galietum		Anthyllideto-Silenetum						Anthyllis vulneraria et Trifolium scabrum				
sous-association	agrostidetosum				koelerietosum	cladonietosum	plantaginetosum	polypodietosum				sanguisorbetosum	cerastietosum					
localité (auteur)	Ameland (Br.-Bl. et de L.)	Terschelling, Vlieland (W.)	Noordwijkerhout (Bb.)	Goeree (Weevers)	Texel (W.)	Wassenaar (Bb.)	Wassenaar (Bb.)	Bergen, Egmond (DK.)	Overveen, Katwijk (Bb.)	Bergen, Katwijk (DK. et Bb.)	Wassenaar (Bb.)	Bloemendaal DK	Katwijk (Bb.)	Goeree (Weevers)	Walcheren (de L.)	Frankrijk (de L.)	Voorne (Bb.)	Belgique (de L.)
nombre de relevés considérés	2	10	4	6	7	7	12	6	8	10	14	6	9	3	10	4	15	9

groupes (voyez texte)

espèce différentielle ¹)



En outre, les espèces suivantes apparaissent dans les relevés repris jusque dans le Tableau III (suivant le nom de l'espèce: 1 le type de végétation sous le numéro de la colonne correspondante, 2 la classe de présence et 3 la valeur la plus fréquente de l'estimation combinée).

Acer pseudoplatanus L. 10 I r
Agropyron littorale Dum. 1 III +; 10 I 2; 11 I r
Agropyron repens (L.) P.B. 2 I ; 11 I r; 15 IV +; 16 V +
Ajuga reptans L. 7 I +; 12 I r
Alchemilla vulgaris L. 15 I +; 16 II +
Ammophila baltica (Fluegge) P. Fourn. 8 I +; 10 I +
Anthriscus scandicina (Web.) Mansf. 18 I +
Anthriscus sylvestris (L.) Hoffm. 12 I r
Bellis perennis L. 15 IV 2; 18 I r
Berberis vulgaris L. 8 I 1
Betula pendula Roth 10 I r
Betula pubescens Ehrh. 11 I r
Brachythecium albicans B. et S. 2 II 1; 4 I 1; 5 I +; 11 I +; 15 I 3
Briza media L. 14 IV 1; 16 II +
Bromus mollis L. 1 V 1; 17 I r; 18 II +
Bryum capillare L. 7 I +; 11 I
Bryum sp. 6 I +; 8 II +; 9 II 1; 12 I +; 13 II 1
Calluna vulgaris (L.) Hull 3 IV 1
Campanula rotundifolia L. 14 IV +
Carduus nutans L. 14 II +
Cardamine hirsuta L. 14 IV +; 15 I r; 18 III +
Carex hirta L. 15 I r
Carex trinervis Degl. 2 II +; 15 I +
Cerastium caespitosum Gilib. 2 II +; 3 II +; 7 I r; 8 II +; 9 II +; 11 IV +; 15 II r
Cerastium tetrandrum Curtis 5 I +
Ceratodon purpureus (L.) Brid. 2 II +; 3 II 2; 8 I +; 11 I +; 13 I +
Cirsium palustre (L.) Scop. 8 I +
Cirsium vulgare (Savi) Ten. 8 I +; 10 II r; 11 II +
Cladonia sect. cladina (Nyl.) Wain. 2 I +; 5 I 2
Cladonia sp. 4 III 1
Clematis vitalba L. 10 I +
Cochlearia danica L. 8 I r; 9 II 1; 11 I 1; 13 II 1; 15 IV +
Cynodon dactylon (L.) Pers. 14 II 1
Cynoglossum officinale L. 10 I +; 12 II +
Cynosurus cristatus L. 2 I +; 15 I +
Dicranella heteromalla (L.) Schimper 11 I +
Didymodon rubellus Br. eur. 9 I +; 11 I +; 12 I +
Ditrichum flexicaule (Schleich.) Hampe var. densum B. et S. 7 I +; 11 I +
Drepanocladus uncinatus (Hedw.) Warnst. 10 I 1
Dryopteris filix-mas (L.) Schott 10 I r
Echium vulgare L. 12 I r; 16 II +
Empetrum nigrum L. 8 I +
Encalypta contorta (Wulfen) Lindb. 11 I +
Epipactis helleborine (L.) Crantz 8 I r; 10 II r
Equisetum arvense L. 2 I +; 10 I +; 15 III r
Erica tetralix L. 5 I +
Erodium glutinosum Dum. 5 I ; 12 I
Erodium sp. 17 I r
Erophila verna (L.) Chevallier 1 III +; 2 I +; 5 I +; 11 I 1; 14 IV 1; 15 IV r; 18 IV +
Eryngium maritimum L. 16 III +
Euonymus europaeus L. 10 I +; 12 IV +
Euphorbia cyparissias L. 18 I r
Euphrasia officinalis L. 14 III +
Eurhynchium striatum (Schreber) Schimper 11 I +

Festuca rubra L. 15 IV 2; 16 V 1

Galium aparine L. 10 I +
Geranium molle L. 12 I +; 15 IV +; 16 IV +; 18 IV 1
Geranium robertianum L. 18 I 1
Geum urbanum L. 8 I +; 10 I ; 12 I +
Glechoma hederacea L. 12 I r

Herminium monorchis (L.) R. Br. 12 I +
Holcus lanatus L. 2 II +; 8 I +; 9 I r; 10 I +; 12 I r; 17 II +
Holcus mollis L. 3 II +
Honckenya peploides (L.) Ehrh. 2 I +
Hypericum perforatum L. 11 I 2

Lathyrus pratensis L. 7 I +; 11 II 1
Leptoglossum retirugum Bull 2 II +
Linaria vulgaris Mill. 10 I +; 12 I +
Listera ovata (L.) R.Br. 10 I +
Lonicera periclymenum L. 11 II 1
Lophocolea heterophylla (Schrad.) Dum. 11 I +
Lycium halimifolium Mill. 15 I r

Medicago arabica (L.) All. 18 I +
Moehringia trinervia (L.) Clairv. 8 I +; 10 I +; 12 II r
Myosotis collina Hoffm. 7 I +; 9 I +; 10 I +; 11 I +; 12 II +; 15 III r; 16 II 1; 18 III +
Myosotis micrantha Pall. 14 II +

Oenothera biennis L. 16 II +
Ophrys aranifera 16 III +
Ornithogalum umbellatum L. 10 I r
Ornithopus perpusillus L. 3 II 2

Phleum arenarium L. 2 I +; 5 III +; 7 II +; 8 I +; 9 I +; 11 III +; 17 I +
Phleum pratense L. 18 I 2
Phleum pratense L. var. nodosum (L.) Richt. 8 I 1; 10 I 1
Pinus silvestris L. 8 II r
Plantago coronopus L. 14 II +; 15 IV +
Polytrichum piliferum Schreber 2 I +; 8 II +
Populus alba L. 16 II +
Populus canescens (Ait.) Sm. 12 I r
Potentilla argentea L. 3 II r; 14 II +
Potentilla reptans L. 12 I +; 15 I +; 16 IV +
Prunella vulgaris L. 11 I +; 12 I r; 14 V +

Ranunculus acer L. 8 II r; 12 I r
Ranunculus repens L. 2 I +
Rhacomitrium canescens (Timm.) Brid. 1 III +
Rhinanthus minor L. 5 I +; 8 IV 1; 10 II 1; 15 I r
Rosa canina L. 7 I r; 10 I r; 11 II r
Rosa eglanteria L. 8 I +; 12 I +; 15 I r
Rumex acetosa L. 8 IV +; 9 II +; 10 II r

Sagina procumbens L. 3 II +; 8 II +
Sambucus nigra L. 10 I r
Sarothamnus scoparius (L.) Wimm. 3 III r
Saxifraga tridactylites L. 10 I r; 12 I +; 14 IV 1; 18 I +
Senecio viscosus L. 10 I +
Sieglingia decumbens (L.) Bernh. 2 I +; 17 I 1
Silene otites (L.) Wibel 8 II r
Sonchus arvensis L. 11 I +
Sorbus aucuparia L. 8 I r; 10 II r
Solanum dulcamara L. 10 I r
Stellaria graminea L. 3 II +
Stellaria media (L.) Vill. 5 I +; 18 I +

Taraxacum agaurum v.S. 6 II +; 7 III +; 14 I +
Taraxacum brachyglossum Dt. 7 I r
Taraxacum lacistophyllum Dt. 2 III +; 5 I +
Taraxacum rubicundum Dt. 6 I +; 7 V +; 11 III +
Taraxacum scanicum Dt. 2 I +
Taraxacum taeniatum H. 6 III +; 7 IV +; 11 III +
Taraxacum tortilobum Flor. 2 II +; 5 II + cf.; 6 I r; 7 I r
Taraxacum sect. vulgaria Schrank 3 II r; 8 I +; 9 III +; 10 II +; 11 IV +; 12 I +; 15 II r
Teesdalia nudicaulis (L.) R. Br. 8 I +; 15 I r

Teucrium scorodonia L. 12 I +
Torilis japonica (Houtt.) D.C. 8 I +
Tortella flavovirens (Bruch) Broth. 7 I +; 9 IV +; 10 I +; 11 II +
Tortula ruralis Ehrh. 11 I +; 13 I +; 18 I +
Tortula subulata (L.) Weber et Mohr 9 IV 1; 10 I +; 11 III +; 13 II +
Tragopogon pratensis L. 5 I +
Trifolium pratense L. 14 IV +; 15 III +
Ulmus carpinifolia Gled. var. suberosa (Moench) Rehd. 15 I r
Urtica dioica L. 10 II r
Valeriana officinalis L. 10 I +
Valerianella locusta (L.) Betcke 18 I +
Veronica arvensis L. 2 I +; 7 I +; 12 II r; 15 IV +; 16 V 1; 18 III +
Veronica teucrium L. 16 V 1
Vicia angustifolia L. 3 III r; 5 I +; 8 I r; 12 I +; 15 V +; 16 V 1; 18 I r
Vicia cracca L. 10 I 1
Vicia hirsuta (L.) S.F. Gray 8 III r; 10 II r; 12 I +; 16 II +
Viola tricolor L. ssp. curtisii (Forst.) Rouy et Fouc. 2 I +; 5 II +; 10 I r; 12 I r

Rumex acetosella, *Trifolium arvense*, *Agrostis tenuis*. Ce sont des différentielles par rapport à l'*A.-S.*, mais elles établissent un lien avec le *Festuceto-Galietum*, si différent à d'autres égards.

La dominance de *Festuca ovina* f. *frisia* et la constance de *Galium verum* ssp. *maritima* constituent entre autres, des caractères communs du *F.-G.* et du *T.-G.* Le *F.-G. koelerietosum* et le *T.-G. cladonietosum* sont les plus proches floristiquement, quoique les différences soient évidentes.

La sous-association à *Botrychium lunaria* (*F.-G. botrychietosum*, DEN HARTOG, 1951) est à la limite des pelouses sèches et humides des dunes. Le même groupement a été décrit auparavant par PREISING (1950) comme l'Ass. à *Botrychium lunaria* et *Polygala vulgaris*. Le *F.-G. molinietosum* (WESTHOFF *et al.*, 1951) est plus ou moins identique avec ce groupement. Les relevés de ces types de transition vers le groupe humide ne sont pas repris dans le Tableau III.

Examinons enfin les groupements des colonnes 17 et 18; il leur manque pratiquement toutes les caractéristiques des associations étudiées. Les relations avec l'*A.-S.* et le *T.-G.* et l'ass. à *Anthy. v.* et *Trif. sc.*, sont indiquées par l'apparition sporadique de *Picris hieracioides*, *Viola rupestris*, et *Potentilla verna*, ainsi que par les espèces plus communes suivantes: *Avena pubescens*, *Cerastium arvense*, *Ononis repens* var. *mitis*, *Ranunculus bulbosus* et *Thymus serpyllum* ssp. *chamaedrys*. Les affinités avec cette dernière association sont sans doute les plus grandes, mais il est peu justifié d'inclure dans celle-ci, ce type de végétation. De même on ne peut, sous prétexte de typification, en faire une association indépendante. On pourrait considérer ces groupements comme des transitions entre les autres associations, mais vu l'absence presque totale de toute caractéristique d'association, il semble préférable, au point de vue nomenclatural, de les classer dans l'alliance, voire même seulement dans l'ordre.

A propos de la position systématique des associations citées plus haut, faisons encore quelques remarques.

Le *Festuceto-Galietum* est généralement classé au sein des *Corynephoretalia* Klika 1934 (DE LEEUW, 1936; TÜXEN, 1937; WESTHOFF *et al.*, 1946). Suite à son étude des îles de Wadden, WESTHOFF (1947) conclut cependant que cette association se trouve juste à la limite entre les *Corynephoretalia* et les *Brometalia*, Br.-Bl. 1936 (i.c. *Koelerion albescentis* (Br.-Bl.) Weevers 1940). Les affinités pour le *Corynephorion* sont mieux marquées dans le *F.-G. agrostidetosum* — (dont les espèces différentielles sont *Agrostis tenuis*, *Rumex acetosella* et localement *Viola* *canina*, *Senecio jacobaea*, *Peltigera canina* et *Sieglingia decumbens*) — que dans le *F.-G. koelerietosum* (différentielles: *Koeleria albescens*, *Rosa pimpinellifolia*, *Calamagrostis epigeios*, *Erigeron acer*, *Euphrasia parviflora* ssp. *curta*, etc.). En 1955 Tuexen ne cite plus le *F.-G.* pour le N. W. de l'Allemagne, mais bien une association vicariante, sinon identique, l'*Agrostideto-Poetum humilis*, qu'il range dans le *Koelerion*. Cette alliance n'est plus classée par Tuexen dans les *Brometalia*, mais bien dans les *Festuco-Sedetalia acris* Tx. 1951.

Dans le *Taraxaco-Galietum*, les espèces du *Corynephorion* apparaissent exclusivement dans la sous-association à *Cladonia foliacea*, où leur rôle est très subordonné. Les espèces du *Bromion* se cantonnent surtout dans la sous-association à *Plantago lanceolata* var. *sphaerostachya*, où elles sont généralement peu abondantes. Par contre les espèces du *Koelerion* sont très répandues, aussi bien dans le *T.-G. cladonietosum* que dans le *T.-G. plantaginetosum;* c'est donc sans hésitation qu'il faut placer l'association dans le *Koelerion albescentis*, en admettant la classification actuelle. Le Prodrome classe l'*Anthyllideto-Silenetum* au sein des *Brometalia erecti* Br.-Bl. 1936. Cette opinion est partagée par Westhoff *et al.* (1946), qui classent cependant l'ass. à *Anthy. v.* et *Trif. sc.* dans le *Koelerion.* Ce dernier point semble contestable. En effet, le *Koelerion* est assez faiblement représenté dans l'ass. à *Anthy. v.* et *Trif. sc.*, tandis que les espèces fluviatiles (la plupart des espèces du *Bromion*) y sont nombreuses. D'un autre côté, on pourrait justifier la place de l'*A.-S.* dans le *Koelerion*, sur base de la haute présence de *Koeleria albescens*, *Lotus corniculatus* var. *ciliatus* cf., *Taraxacum* div. esp., etc., ainsi que par la présence de plusieurs espèces pouvant passer comme différentielles par rapport au *Bromion* (*Ammophila arenaria*, *Senecio jacobaea*, *Rubus caesius*, *Galium verum* ssp. *maritimum*, *Festuca ovina* f. *frisia*, *Festuca rubra* subv. *arenaria*, etc.).

Doing Kraft (comm. prov.) préconise une solution plus radicale: le *Koelerion*, limité aux groupements non fermés, formerait un ordre nouveau ("*Avenetalia pubescentis*") avec certaines associations herbeuses du domaine atlantique ou même subatlantique, rattachées actuellement aux ordres des *Brometalia* et en partie aussi des *Arrhenatheretalia.* Cet ordre serait caractérisé entre autres, par une humidité atmosphérique plus importante, et en genéral aussi par un sol plus profond que chez les *Brometalia.* Nous ne pouvons examiner maintenant cette classification, dans laquelle sans aucun doute doivent prendre place l'ass. à *Anthy. v.* et *Trif. sc.* et l'*A.-S.*, ainsi que les groupements repris dans les colonnes 17 et 18 (Tableau III).

A cet égard, nous estimons que le moment n'est pas encore venu de ventiler les espèces en caractéristiques d'alliance, d'ordre et de classe; c'est la raison pour laquelle dans le Tableau III, nous distinguons, à côté des caractéristiques locales des associations et des différentielles des sous-associations, seulement certains groupes d'espèces, communs entre les diverses associations.

5. CARACTÉRISTIQUES ÉCOLOGIQUES DES ASSOCIATIONS, SOUS-ASSOCIATIONS ET VARIANTES

Nous avons décrit les profils de sol et examiné des échantillons de certains individus du *T.-G.* et de l'*A.-S.* Les différences dans les profils de ces deux associations sont faibles. L'horizon Ao est le mieux développé dans l'*A.-S. polypodietosum* (variante à *Salix repens*), mais peut se présenter également dans *T.-G. plantaginetosum*. Il manque le plus souvent chez les autres groupements. Cet horizon ne dépasse jamais quelques millimètres d'épaisseur. L'horizon A1, d'une puissance de 6 à 10 cm, est gris-noir à gris et passe vers le bas graduellement à l'horizon A2, qui est gris-blanc. La limite entre ces deux horizons est souvent difficile à tracer. De même, la limite inférieure de l'A2 est peu nette; elle fut considérée à 20–25 cm au cours de l'échantillonage. Sur les pentes, le profil est quelquefois perturbé par des fouilles, des effondrements, ou des glissements de sol (lapins) et dans quelques cas on rencontre des superpositions de plusieurs profils ou parties de profils (accumulation éolienne).

Au cours de l'étude pédologique, limitée à la région comprise entre Scheveningen et Noordwijk, nous avons prélevé des échantillons de 14 groupements; à une exception près, les horizons A1 et A2, ont été analysé.

On a déterminé les éléments suivants: le pH(H_2O et KCl), $CaCO_3$–%, P total–%; N total–% et humus–%, et N total/humus.

Les résultats des analyses de sol sont consignés dans les Tableaux I et II, pour autant qu'ils se rapportent aux végétation y renseignés. Tous les résultats de l'étude pédologique sont repris dans le Tableau IV, en plus des moyennes on y a figuré les extrêmes, au cas où plus d'une analyse fut effectuée par type de végétation.

La majorité des groupements analysés se trouve entre Scheveningen et Wassenaar. La variante à *Salix repens* de l'*A.-S. polypodietosum*, développée ici sous forme d'une sous-variante à *Gentiana cruciata* (Tableau IV, colonne 3), montre un pH assez élevé pour l'horizon Al, soumis à de faibles variations. La teneur en carbonates de Calcium, subit les fluctuations les plus importantes (1,1–2,7 %). Le pH et la teneur en carbonates sont plus élevés dans l'A2, le pourcentage d'humus est notablement plus faible. L'analyse d'une végétation comparable, sur un versant N, entre Katwijk et Noordwijk (facies à *Salix repens*, colonne 2), livre pour le pH et la teneur en carbonates, des valeurs semblables aux analyses précédentes, mais le pourcentage en humus de l'horizon A1 et le pourcentage en P total des horizons A1 et A2, sont nettement plus élevés. Au total, l'évolution du profil y est plus avancée, ce qui s'explique vraisemblablement par l'état plus serré, en pelouse, de la végétation à cet endroit. Lorsque, dans cette même région, *Salix repens* manque dans l'*A.-S. polypodietosum*, il semble que la maturation du profil soit moins avancée (colonne 1), et la ressemblance avec l'*A.-S.* des dunes, entre Scheveningen et Wassenaar, devient plus grande.

Dans son ensemble, l'*A.-S. polypodietosum* présente dans son horizon A1, un pH KCl légèrement supérieur à 7, une teneur en carbonates toujours supérieure à 1 %, (généralement ± 1,5 %), et un pourcentage en humus variant de 2 à 5 %. Dans l'horizon A2, le pH KCl est généralement un peu supérieur à 7,5, la teneur en carbonates ne descend plus en-dessous de 2 % (généralement env. 3 %) tandis que le pourcentage en humus oscille autour de 1 %.

Ces valeurs de l'*A.-S polypodietosum*, semblent valables aussi pour le

TABLEAU IV
Résultats des analyses pédologiques

association	Anthyllideto-Silenetum				Taraxaco-Galietum			
sous-association	polypodietosum				plantaginetosum		cladonietosum	
variant à		Salix repens						
sous-variant à			Gentiana cruciata					
horizon A1								
nombre d'échantillons . .	1	1	6		3		3	
limite inférieur en cm . .	6	8	9.5	6/14	8	6/9	10	10
pH H_2O	7.4	7.3	7.4	7.2/7.7	7.6	7.6/7.7	7.0	6.8/7.3
pH KCl	7.1	7.1	7.3	7.1/7.4	7.1	6.9/7.3	6.6	6.3/7.0
$CaCO_3$-%	1.7	1.4	1.8	1.1/2.7	1.4	1.3/1.5	0.4	0.2/0.6
P total-%	0.04	0.08	0.03	0.02/0.04	0.04	0.03/0.05	0.04	0.03/0.05
N total-%	0.11	0.18	0.09	0.07/0.12	0.13	0.10/0.15	0.13	0.09/0.19
humus-%	3.4	4.9	2.7	2.1/3.5	3.2	2.6/3.8	3.7	2.7/5.4
N total/humus × 100 . .	3.2	3.7	3.3	3.0/3.7	4.0	3.8/4.2	3.3	3.2/3.4
horizon A2								
nombre d'échantillons . .	1	1	6		3		2	
limite inférieur en cm . .	25	25	22	18/25	19	18/20	22	20/24
pH H_2O	8.1	8.2	7.8	7.4/8.3	7.9	7.7/8.1	7.6	7.5/7.7
pH KCl	7.6	7.7	7.6	7.4/7.7	7.4	7.1/7.6	7.2	7.1/7.3
$CaCO_3$-%	2.9	3.4	2.9	2.0/3.7	3.0	2.6/3.6	1.8	0.9/2.7
P total-%	0.03	0.05	0.03	0.02/0.03	0.03	0.02/0.03	0.03	0.02/0.03
N total-%	0.03	0.02	0.03	0.01/0.05	0.03	0.02/0.04	0.03	0.01/0.05
humus-%	1.0	0.8	0.8	0.6/1.5	1.0	0.8/1.3	1.0	0.6/1.4
N total/humus × 100	3.0	2.5	2.7	1.7/3.3	3.0	2.2/3.7	3.1	2.5/3.6

T.-G. plantaginetosum. (colonne 4). La comparaison des moyennes de ce dernier type et de l'*A.-S. polypodietosum*, dans la même région (colonne 3), montre que la teneur en carbonates de l'horizon A1, est un peu plus faible, la teneur en humus un peu plus forte. Les différences sont bien plus nettes entre le *T.-G. plantaginetosum* et le *T.-G. cladonietosum*, le pH de l'horizon A1, ne dépasse plus 7, la teneur en carbonates est toujours inférieure à 1 % et les teneurs en humus peuvent atteindre des valeurs plus élevées (jusque 5,5 %).

L'horizon A2 montre également une décalcification nette, de sorte qu'ici le pourcentage en carbonates peut descendre sous 1 %; le pH KCl est encore supérieur à 7, la teneur en humus est d'environ 1 %.

En résumé, nous constatons que les différences pédologiques entre les variantes de l'*A.-S. polypodietosum*, sont faibles, du moins dans le cadre de nos analyses; et que les facteurs édaphiques expliquent tout aussi peu la différence existant entre l'*A.-S. polypodietosum* et le *T.-G. plantaginetosum*; enfin qu'il existe une corrélation nette entre certains facteurs édaphiques et les sous-ass. du *T.-G.* (*plantaginetosum*, *cladonietosum*).

La grande différence floristique entre l'*A.-S. polypodietosum* et le *T.-G. plantaginetosum* est probablement due à des facteurs d'ordre microclimatologique. En effet, le premier groupement est lié exclusivement à des versants N, le deuxième est cantonné pratiquement dans les pannes. L'insolation est bien moins intense sur les pentes exposées au N, que dans les vallées des dunes. Ceci influence aussi bien la radiation totale reçue au sol; que sa distribution au cours de l'année, la température de l'air et du sol, l'humidité absolue et relative de l'air et peut-être l'humidité du sol.

Nous n'avons pas procédé à des mesures microclimatiques, mais il est hors de doute, que les oscillations des facteurs climatiques, sont de bien plus faibles amplitudes sur les versants N que dans les vallées. En général, il y règne un microclimat plus humide et plus atlantique que dans les dépressions, ainsi que l'atteste le grand nombre de mousses dans l' *A.-S. polypodietosum* (VAN DIEREN, 1934).

On peut justifier de la même façon, la différence entre l'*A.-S. polypodietosum* et l'*A.-S. cerastietosum* entre Katwijk et Noordwijk. Mais il est difficile d'expliquer pourquoi dans cette région se développe l'*A.-S. cerastietosum* dans les zones planes, tandis qu'entre Scheveningen et Wassenaar, c'est le *Taraxaco-Galietum* que l'on note dans les vallons des dunes; des facteurs historiques entrent peut-être ici en jeu.

Déjà plus haut, nous avons attiré l'attention sur le caractère plus fermé de l'*A.-S. polypodietosum* des dunes entre Katwijk et Noordwijk, en comparaison avec le même groupement de la région de Wassenaar. D'une manière plus générale, les dunes de cette zone se distinguent de celles des autres côtes néerlandaises, par l'absence presque totale d'arbustes et d'arbres. On n'y trouve pas *Betula pubescens* et *B. pendula*, *Crataegus monogyna* est rare, et même *Hippophae rhamnoides*, par ailleurs si répandu, est ici nettement moins bien représenté. De même les arbrisseaux de *Salix repens* et de *Ligustrum vulgare* y sont beaucoup moins communs, que par exemple au N de Scheveningen. La végétation des pentes N et des pannes y est constituée généralement d'une pelouse bien fermée de graminées et de plantes herbacées basses, qui physionomiquement donne l'impression d'être pâturée. Cependant, à notre connaissance, aucun pâturage n'a eu lieu depuis les dernières décades. Certes, cette région est visitée par de nombreuses personnes, et le piétinnement y est beaucoup plus important que dans les autres régions étudiées. De même il est reconnu que la densité des lapins y a été particulièrement grande, avant la déclaration de la myxomatose.

On pourrait expliquer par ces facteurs, l'abondance relative de *Cerastium arvense*, *Achillea millefolium*, *Anthoxanthum odoratum*, *Hypochoeris radicata*, *Bromus mollis* et *Rosa pimpinellifolia*. De plus, on peut supposer que le voisinage des villages de pêcheurs, Katwijk et Noordwijk, et de l'arrière-pays d'horticulture, a systématiquement bloqué le développement des essences ligneuses. Les besoins en bois, aussi bien pour le chauffage que pour la clôture des champs (argousier, duindoorn) ont été ici très grands dans les siècles passés, et la zone des dunes y est plus étroite que dans les régions avoisinantes.

De même on n'échappe pas aux spéculations, lorsqu'il s'agit d'expliquer les variantes ou sous-variantes, qui sont souvent remarquables, et qui reposent le plus souvent sur la présence ou l'absence d'une ou de plusieurs espèces (*Gentiana cruciata*, *Anthyllis vulneraria*, *Satureja acinos* et *S. vulgaris*, *Knautia arvensis*, etc.).

A notre sens, il s'agit plus d'un problème phytogéographique qu'écologique. Plusieurs espèces présentent dans la région des dunes, une distribution remarquable; elles sont très abondantes localement, et manquent totalement ou presque à peu de distance au nord ou au sud. Ainsi *Rosa pimpinellifolia* est très commun à Bergen, à Haarlem et entre Noordwijk et Katwijk, mais est connu de quelques stations seulement entre le Wassenaarse Slag et Scheveningen. Dans cette dernière région *Gentiana cruciata* est plus ou moins commun; il est sporadique entre le Wassenaarse Slag et Katwijk, et manque ailleurs complètement dans la région des dunes (l'espèce était connue dans les dunes près de Overveen au siècle dernier).

On pourrait citer bien d'autres exemples. Dans le District des Dunes, plusieurs régions se distinguent entre elles floristiquement; et l'on est parfois tenté de faire une comparaison avec les îles de Wadden, dont les différences floristiques s'expliquent en partie par leur isolement. Les variations édaphiques et climatologiques observées dans les diverses régions, sont impuissantes, dans la plupart des cas, à justifier ce phénomène. Il ne semble pas impossible, en effet, que la dispersion active de plusieurs espèces dans notre dition, ne soit nullement terminée, mais se trouve peut-être encore dans une phase relativement jeune. On ne considérera pas ici seulement la jeunesse du paysage des dunes récentes, mais aussi le fait, que jusque tout récemment, les dunes étaient très mobiles et n'offraient certes pas une station favorable à la plupart des espèces en cause. La présence et l'absence de certaines plantes dans des stations écologiquement semblables, seraient la conséquence d'un premier établissement, puis d'une dispersion de l'espèce.

C'est dans ce sens qu'il faut chercher l'explication des peuplements assez aberrants de Bloemendaal, caractérisés par l'abondance de *Rosa pimpinellifolia* et *Sanguisorba minor* (*A.-S. sanguisorbetosum*).

Le *Taraxaco-Galietum* est favorisé par la dent des lapins et un certain piétinnement, et ceci est encore plus vrai pour le *Festuceto-Galietum*. Cependant le *F.-G.*, plus que le *T.-G.*, est conditionné par des facteurs pédologiques plutôt que par des différences dans l'intensité et le genre de pâturage.

Westhoff (1947, msc.) a effectué quelques analyses pédologiques du *F.-G. koelerietosum* de Texel (3) et du *F.-G. agrostidetosum* de Vlieland et Terschelling. Il examina l'horizon de 2 à 8 cm. La teneur en carbonates (en majorité $CaCO_3$; 0,1–0,4 %, moyenne 0,3 %) et le pH H_2O (6,0–6,7, moyenne 6,5), étaient les plus élevés dans le *F.-G. koelerietosum*. Dans le *F.-G. agrostidetosum*, la teneur en carbonates varie de 0,03 % à 0,12 %, (moyenne 0,06 %) et le pH de 5,4 à 6,3 (moyenne 6,0). On constate donc une diminution des pourcentages des carbonates et du pH dans l'ordre suivant: *T.-G. plantaginetosum*, *T.-G. cladonietosum*, *F.-G. koelerietosum*, *F.-G. agrostidetosum*, (cf. Tableau IV, colonne 4 et 5, horizon A1). Les principales différences phytosociologiques sont parallèles à ces phénomènes. De même que dans le *T.-G.*, la teneur en humus du *F.-G.* est la plus élevée dans la sous-association pauvre en calcaire; dans le *F.-G. koelerietosum* cette teneur est de 2–4 % (moyenne 3,2 %) contre 2,5 5,5 % (moyenne 4,2 %) dans le *F.-G. agrostidetosum*. Le *F.-G.* de Goerce, qui comporte aussi bien des éléments du *koelerietosum* que de l'*agrostidetosum*, a selon Weevers (1940), un pH d'environ 6,0, ce qui concorde avec les données précédentes.

L'association à *Anthyllis vulneraria* et *Trifolium scabrum* est notée aux expositions chaudes des vieilles digues dans la zône côtière, "là surtout, où la digue est constituée par un mélange d'un peu d'argile et de beaucoup de sable calcarifère" (Weevers). Le pâturage est toujours plus ou moins intense, ce qui se traduit clairement dans la végétation.

Ce milieu s'écarte notablement de celui du *T.-G.* et du *F.-G.*, par le pâturage plus sévère et la richesse en particules fines (argile) partiellement aussi par la teneur plus élevée en calcaire. L'ass. à *Anthy. v.* et *Trif. sc.* possède en commun avec l'*A.-S.* un sol riche en calcaire, mais il est remarquable de constater que la première association se rencontre surtout à l'exposition S, la deuxième à l'exposition N. Notons, en parfaite concordance avec ces faits, que les deux associations possèdent un certain nombre d'espèces, dites calcicoles, tandis que les éléments du *Polypodieto-Empetretum*, qui transgressent fortement dans l'*A.-S. polypodietosum*, ainsi que les nombreuses mousses de l'*A.-S. polypodietosum*, manquent dans l'ass. à *Anthy. v.* et *Trif. sc.* D'un autre côté, on peut supposer qu'il existe une certaine compensation entre le microclimat plus humide de l'*A.-S.* et le bilan hydrique meilleur du sol plus argileux de l'ass. à *Anthy. v.* et *Trif. sc.*

6. Distribution des groupements étudiés

Les quatre associations étudiées plus haut, sont toutes cantonnées dans le secteur boréo-atlantique. Le *Festuceto-Galietum* possède l'aire la plus vaste. Aux Pays-Bas, le *F.-G.* est surtout connu du district de Wadden. Au sein de ce district, la teneur en calcaire du sable des dunes, n'est pas partout également faible et dans la plupart des cas, ce facteur détermine la sous-association, d'une manière sans doute décisive. On rencontre le *F.-G. agrostidetosum* dans les régions les plus pauvres en calcaire, soit à Ameland (Braun-Blanquet et de Leeuw, 1936), Terschelling (Westhoff, 1947), Vlieland (idem; de Vries, 1950) et peut-être à Schoorl (cf. de Leeuw, 1938). Par contre le *F.-G. koelerietosum* domine sur l'île de Texel, relativement riche en calcaire. (Westhoff, 1947; den Hartog, 1951). Nous ne connaissons malheureusement aucun relevé de Schiermonnikoog, la zône la plus calcaire du District de Wadden, où ce groupement existe sans aucun doute.

En dehors du District de Wadden, le *F.-G.* a été signalé, assez tôt dans les dunes de l'intérieur, par DE LEEUW (1938) de Noordwijkerhout et par WEEVERS (1940) de l'ancien paysage de Goeree. Nous mêmes avons trouvé cette association à Noordwijkerhout (cf. Tableau III, colonne 3) et à Loosduinen (relevés inédits). Dans les dunes intérieures, on note aussi bien la sous-association à *Agrostis tenuis* (par ex. à Noordwijkerhout) que celle à *Koeleria albescens* (ex. Loosduinen).

Enfin, dans les jeunes dunes, on ne trouve que localement le *F.-G. koelerietosum*, dans des vallées sèches, fortement décalcifiées, entre autres près de Bloemendaal et De Zilk (relevés personnels inédits). Cependant, en règle générale, les vallées sont occupées ici par le *Taraxaco-Galietum*.

L'aire du *F.-G.* s'étend en dehors de notre pays, aussi bien vers le nord-est que vers le sud-ouest. TUEXEN (1937) signale le groupement, sous forme de pâture à moutons dans les anciennes dunes des îles septentrionales et orientales de la Fries, où des éléments plus continentaux s'introduisent dans l'association: *Dianthus deltoides* et *Thymus serpyllum* ssp. *angustifolius*.

Cette tendance est encore plus accentuée dans le *F.-G.* du Danemark. En plus des deux espèces précitées, IVERSEN (1936) signale dans les pelouses sèches des dunes de Skallingen, *Silene otites*, tandis que *Koeleria albescens*, élément atlantique, y est remplacé par *Koeleria glauca*, nettement continental. En même temps, le rôle joué dans le *F.-G.* des Pays-Bas par *Festuca ovina*, diminue en importance; en plus de *Agrostis tenuis*, les dominants sont ici *Sieglingia decumbens* ou *Festuca rubra*, sous-var. *arenaria*. A Tvaersted (Jutland septentrional) on note dans les relevés de BÖCHER (1954, Tableau III, no. 11 et 12) encore d'autres espèces à distribution continentale, notamment *Knautia arvensis* et *Geranium sanguineum* (abondant). Quoique ces groupements danois montrent une similitude nette avec le *F.-G. agrostidetosum*, on peut se demander s'il ne convient pas de les classer dans une association différente (vicariante).

On rencontre aussi au voisinage de Kattegat et de Oostzee, des groupements qui relèvent sans doute du *F.-G.* Nous visons ici la côte nord de Sjaelland (BÖCHER, 1945) et le "Lübecker Bucht" (ONNO, 1933, "Festucetum ovinae"). La présence locale dans ces groupements de *Armeria vulgaris*, *Plantago maritima* et de *Honckenya peploides*, est remarquable.

En direction du sud-ouest, le long de la côte belge, on trouve le prolongement du *F.-G.*, qui est connu des anciennes dunes des îles hollandaises méridionales et zéelandaises. L'association peut s'y développer, aussi bien à partir de groupements du *Koelerion*, suite à un lessivage intense et profond du sol, que directement à partir de placages de sables pauvres en carbonates, déposés localement à l'occasion de rupture de digues. (Sable à *Cardium*, LEBRUN *et al.*, 1949). Les données les plus méridionales proviennent de Lombartzijde et de Westende (MASSART, 1907–1908; LOUIS et LEBRUN, 1942). Le *F.-G.* est inconnu de la côte française du Canal.

La présence du *F.-G.* en Angelterre n'est pas encore certaine. Les publications de Pearsall (1934), Tansley (1949) et Salisbury (1952) permettent quelques conclusions en ce sens.

Le *F.-G.* semble manquer en Irlande, dont la végétation a été récemment étudiée et décrite en partie par divers auteurs.

Bien plus restreinte est l'aire du *Taraxaco-Galietum*, que l'on peut, en gros, considérer comme une association vicariante du *F.-G.*, dans le District des Dunes, du continent hollandais. Quoique la description donnée au Ch. 3, soit principalement basée sur des groupements rencontrés entre Scheveningen et le Wassenaarse Slag, l'association s'étend aussi ailleurs dans le District des Dunes, d'une manière plus ou moins générale. Elle manque cependant entre Katwijk et Noordwijk. Les deux sous-associations ne semblent pas liées à une partie quelconque de l'aire.

On ne doit pas s'attendre à trouver le *T.-G.* en dehors de la Hollande, étant donné que les caractères les plus spécifiques de l'association (richesse en espèces et individus de *Taraxaca*, et présence constante de *Viola rupestris*) sont particuliers au District des Dunes en Hollande. Il existe certes, une parenté évidente avec d'autres groupements du *Koelerion*, notamment avec le *Tortuleto-Phleetum ononidetosum* Heinemann, des dunes belges (Lebrun *et al.*, 1949). L'association à *Viola curtisii* et *Syntrichia ruralis*, décrite de l'Irlande par Braun-Blanquet et Tuexen, est une vicariante du *Tortuleto-Phleetum* des dunes continentales; les relevés dans lesquels *Tortula ruralis* joue un role subordonné, montrent en effet une affinité avec le *T.-G.* (Braun-Blanquet et Tuexen, 1952, Tableau 46). A ce propos on consultera également Böcher (1954).

De même, il existe une certaine parenté avec les pâturages des dunes écossaises ("machair"), ces derniers sont en général plus pauvres en espèces et abritent plus d'éléments typiques des prairies, mais peuvent avoir plusieurs espèces du *T.-G.* entre autres: *Linum catharticum*, *Polygala vulgaris*, *Achillea millefolium*, *Thymus serpyllum*, *Avena pubescens*, *Carex flacca*, *Galium verum*, etc. (Barkman, 1950; MacLead, 1951; Gimingham *et al.*, 1951).

L'*Anthyllideto-Silenetum* est également cantonné à la région des dunes entre Bergen et la Haye. La largeur des dunes est ici remarquablement large. Ce facteur est important, car l'association n'atteind son développement optimum qu'à une certaine distance de l'estran. Entre Scheveningen et Katwijk, l'*A.-S.* se trouve surtout dans une zône située à 300–1000 m de l'estran; entre Katwijk et Noordwijk, l'association sous une forme quelque peu appauvrie, s'avance plus près de la mer.

L'*A.-S. polypodietosum* existe dans toute la région. De même, la variante à *Salix repens* se rencontre partout, mais est rare entre Katwijk et Noordwijk. Les deux autres sous-associations ont une distribution très locale: l'*A.-S. cerastietosum* est principalement localisé dans les dunes entre Katwijk et Noordwijk, l'*A.-S. sanguisorbetosum* dans les dunes de Bloemendaal. Nous avons déjà signalé le caractère local des sous-variantes.

Le fait que l'*A.-S.* manque dans les dunes du continent au sud de la Haye, s'explique problablement par leur médiocre largeur et peut aussi être la conséquence d'une influence humaine plus intense. Il est cependant remarquable que plus au sud, l'*A.-S.* manque dans sa forme caractéristique, quoique des fragments existent encore dans la zône étendue des dunes de Voorne. Plusieurs espèces les plus typiques manquent ici, ou sont notablement plus rares: (*Gentiana cruciata*, *Orobanche picridis*, *Satureja acinos*, *Viola rupestris*, *Arabis hirsuta*, *Erigeron acer*, *Picris hieracioides*). Dans la région des estuaires, d'autres espèces transgressent aussi bien dans l'ass. à *Anthy. v.* et *Trif. sc.* (entre autres *Carlina vulgaris* et *Ranunculus bulbosus*). A la côte belge, l'association à *Anthyllis maritima* et *Thesium humifusum* Heinemann, remplace l'*A.-S.* (Lebrun *et al.*, 1949). La limite septentrionale de l'*A.-S.* se trouve à Bergen. Dans le District de Wadden, l'*A.-S. polypodietosum* est remplacé par le *Polypodieto-Empetretum* et l'association à *Salix repens* et *Thalictrum minus* (Schiermonnikoog). Les espèces du *Bromion*, caractéristiques de l'*A.-S.* manquent ici presque totalement.

Le long de la côte danoise, la teneur en carbonates du sable des dunes, est localement plus élévée, et l'on y retrouve dans les pelouses fermées un nombre remarquable d'espèces du *Bromion* et à aire souvent continentale.

Quoique ces groupements rappelent l'*A.-S.*, les différences floristiques sont grandes. On remarque dans les pelouses des dunes à Bulbjerg, Hjörring et Tvaersted (Jutland septentrional) entre autres les espèces suivantes: *Geranium sanguineum* (très commun), *Thymus serpyllum* ssp. *angustifolius*, *Koeleria glauca*, *Artemisia campestris*, *Thalictrum minus* var. *dunense*, *Potentilla verna*, *Pulsatilla pratensis*, *Anthyllis vulneraria* et *Pimpinella saxifraga* (Böcher, 1954; Barkman *et al.*, 1956).

Ces groupements du Jutland septentrional présentent avec l'*A.-S.* une différence importante, en ce que les espèces généralement répandues dans le *Corynephorion* de l'Europe occidentale, sont ici plus abondantes. D'un autre côté, certaines des espèces citées plus haut, semblent transgresser dans le *F.-G. agrostidetosum* ou dans des groupements vicariants de Skallingen, de sorte que la limite entre pelouses sur substrat plus ou moins riche ou pauvre en carbonates, semble ici plus difficile à tracer que dans la zône côtière néerlandaise.

Des dunes parfois très riches en calcaire se rencontrent en divers endroits de la côte anglaise et écossaise. Elles y sont le plus souvent pâturées, et de plus les lapins y étant très nombreux, avant la myxomatose, les dunes moins jeunes portent en général une pelouse fermée. Les arbustes y sont rares. Quoique ces pelouses aient en commun plusieurs espèces, les différences locales sont importantes, et comme chez nous, chaque région a ses spécialités (Hepburn, 1944). Ainsi *Rosa pimpinellifolia* est également très localisé dans les dunes anglaises. Il est difficile de se faire une idée exacte des groupements de ce pays, car les relevés d'individus d'association manquent, et la littérature anglaise cite une liste synthétique de plantes croissant dans une zône déterminée. Un grand nombre d'espèces de l'*A.-S.* se rencontrent dans les dunes calcaires d'Angleterre et d'Ecosse, ainsi *Anthyllis vulneraria*, *Botrychium lunaria*, *Arabis hirsuta*, *Carlina vulgaris*, *Erigeron* *acer*, *Pimpinella saxifraga*, *Ranunculus bulbosus* et *Thalictrum minus* (HEPBURN, 1944; TANSLEY, 1949; GIMINGHAM, 1951; SALISBURY, 1951). D'un autre côté, des graminées communes dans l'*A.-S.* y font défauts (*Calamagrostis epigeios*, *Avena pubescens*, *Koeleria albescens*) ou y sont du moins beaucoup plus rares. De même, *Koeleria gracilis*, vicariant en certaines régions, et peu commun. Vu le grand nombre d'espèces communes, et le milieu analogue, WESTHOFF *et al.*, (1946) ont conclu à la présence de l'*A.-S.* dans les dunes calcaires d'Angleterre. Des recherches ultérieures sont nécessaires pour confirmer cette hypothèse.

L'*A.-S.* manque en Irlande; un groupement affine, l'association à *Camptothecium lutescens* et *Asperula cynanchica*, Br.-Bl. et Tx. 1952, est décrit de la côte occidentale.

Enfin l'association à *Anthyllis vulneraria* et *Trifolium scabrum* est notée dans sa forme la plus riche, dans les îles sud-hollandaises et zéelandaises. Ici se rejoignent les deux voies d'immigration, par où les espèces méditerranéennes et les espèces continentales ont pu atteindre nos dunes: d'une part la côte franco-belge formée dans sa partie septentrionale par des formations calcaires et des sables calcarifères, d'autre part les grandes rivières: Rhin, Meuse et Escaut.

L'extension de cette association au-delà de cette région, ne peut encore être déterminée avec certitude. Quelques relevés, pris par DE LEEUW à la côte française dans le Nord (Franceville et Le Home), sont rapportés à l'ass. à *Anthy. v.* et *Trif. sc.* (Tableau III, colonne 16); des groupements semblables ont été notés également en Belgique, notamment à Breedene et à Mariakerke.

LEBRUN *et al.* (1949) ne mentionnent pas l'association. Il est nécessaire de mieux préciser d'abord les limites de notre association avec l'ass. à *Anthyllis vulneraria* et *Thesium humifusum*.

L'ass. à *Anthy. v.* et *Trif. sc.* n'a pas été observée au nord de la région des estuaires.

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JAARBOEK 1956

VERSLAGEN EN MEDEDELINGEN

DER

KONINKLIJKE NEDERLANDSE BOTANISCHE
VERENIGING
OVER HET JAAR 1956

UITGEGEVEN 1 JUNI 1957

KONINKLIJKE NEDERLANDSE BOTANISCHE VERENIGING
AMSTERDAM

KONINKLIJKE NEDERLANDSE BOTANISCHE VERENIGING
(Opgericht 15 augustus 1845)

BESTUUR in 1956

Prof. Dr. J. Lanjouw, voorzitter
Dr. S. J. van Ooststroom, ondervoorzitter
Dr. A. Quispel, 1e secretaris
Mej. Dr. J. de Zeeuw, 2e secretaresse
Prof. Ir. J. L. van Soest, penningmeester

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JAARVERSLAG VAN DE EERSTE SECRETARIS OVER 1956

Wanneer wij de lotgevallen van onze vereniging in het jaar 1956 willen bespreken zal allereerst onze aandacht moeten gaan naar hen, die ons dit jaar door de dood ontvielen. Ons bereikte het bericht, dat op 25 februari 1956 ons corresponderend lid E.D. Merrill overleed, terwijl wij onder de gewone leden het verlies moeten betreuren van Dr. A.J.Kluyver en M.J.van Sambeek.

Elmer Drew Merrill heeft op velerlei wijze belangrijke bijdragen voor de ontwikkeling der plantkunde geleverd. Sinds 1902 werkte hij als plantkundige aan het „Bureau of agriculture" te Manilla op de Philippijnen, sinds 1906 aan het „Bureau of science" aldaar. Hij heeft enorme verdiensten gehad voor de vermeerdering der kennis van de flora van dit gebied en heeft aldaar een spoedig beroemd geworden herbarium en bibliotheek gesticht. Hoewel hij in 1919 algemeen directeur werd van het Bureau of Science en dus zeer veel tijd aan andere gebieden dan dat der plantkunde moest besteden verschenen toch nog van zijn hand de vier omvangrijke delen van de „Enumeration of Phillipine flowering plants". In 1923 verliet hij de Philippijnen voor zijn benoeming tot deken van de Universiteit van California, een functie, die hij in 1930 verwisselde voor die van directeur van de „New York Botanical Garden", waarna hij in 1935 directeur werd van het Arnold Arboretum te Harvard. Naast zijn grote verdiensten op wetenschappelijk en organisatorisch gebied moet hier ook vermeld worden het grote aandeel, dat hij heeft gehad in de internationale organisatie der biologische wetenschappen. In 1935 werd hij tot corresponderend lid van onze vereniging benoemd.

Het zou onjuist zijn bij de herdenking van Dr. A.J.Kluyver alleen zijn verdiensten op botanisch gebied te memoreren. In hem verloor ons land immers een zijner meest vooraanstaande natuuronderzoekers, wiens naam over de gehele wereld met waardering genoemd werd. Na in Delft gestudeerd te hebben werd hij als assistent verbonden aan het laboratorium voor technische botanie te Delft, waar hij in 1914 promoveerde. Spoedig hierop volgde zijn benoeming tot nijverheidsconsulent in Indie. In 1921 werd hij benoemd tot opvolger van Beyerinck als hoogleraar in de microbiologie aan de technische hogeschool te Delft. Het is ondoenlijk en ook onnodig de grote verdiensten te schetsen, die hij in deze functie heeft getoond te bezitten. Het groot aantal dissertaties en publikaties, die onder zijn leiding verschenen, spreken in dit opzicht duidelijker taal en deze publikaties hebben ook internationaal de waardering gevonden, die hen toekwam. Vele Nederlandse biologen hebben het onschatbare voorrecht gehad tijdens hun studietijd of daarna enige tijd onder zijn leiding in de bijzondere sfeer van zijn laboratorium te mogen werken. Zonder uitzondering zal ieder van hen aan deze periode terugdenken als aan een der hoogtepunten van zijn opleiding tot bioloog of biochemicus, een hoogtepunt door de wetenschappelijke belangstelling, die hij wist te wekken en die bij hem steeds met een warme menselijke belangstelling gepaard ging.

De Heer M. J. van Sambeek was nog slechts korte tijd lid van onze vereniging, doch zijn verdiensten op botanisch gebied zijn reeds van veel oudere datum. Als onderwijzer heeft hij in de geest van Heimans en Thijsse zeer veel bijgedragen om bij zijn leerlingen belangstelling te wekken voor de schoonheid van het Twentse landschap en de kennis van flora, fauna en geologie. Op 11 juni 1923 werd op zijn initiatief te Enschede de „Enschedese Museumvereniging" opgericht. Door zijn onvermoeide ijver en zijn stimulerende invloed op anderen groeiden de collecties hiervan tot in 1939 deze collectie een waardige omgeving kreeg bij de opening van het Natuurhistorisch Museum. Hij werd hiervan tot directeur benoemd, een functie, die hij tot 1948 vervuld heeft.

Wij gedenken met dankbaarheid het werk van hen, die op zo uiteenlopende wijze hun beste krachten aan biologisch onderzoek hebben gewijd.

De gebruikelijke wijziging in de bestuurssamenstelling had dit jaar een ongebruikelijk verloop, doordat een aantal leden zich niet konden verenigen met de door het bestuur voor het voorzitterschap kandidaat gestelde personen. Deze leden stelden een tegenkandidaat voor met de argumentering, dat men er prijs op stelde een systematicus als voorzitter te zien. Op de jaarvergadering, die ten gevolge van deze tegenkandidatuur een maand moest worden uitgesteld (om de termijn van kandidaat- en tegenkandidaatstelling te laten voldoen aan de eisen der statuten) werd de tegenkandidaat Dr. J. Lanjouw als nieuwe voorzitter gekozen en trad Dr. E. van Slogteren als voorzitter af. Namens het bestuur dankte Dr. S. J. van Ooststroom en namens de vergadering Dr. V. J. Koningsberger de scheidende voorzitter voor het vele en buitengewoon belangrijke werk, dat hij voor de vereniging heeft gedaan.

Het aantal leden van de vereniging vertoonde in 1956 wederom een toename. Op 31 december 1956 bedroeg het aantal leden 508, tegen 486 in het begin van het jaar. Hiervan zijn 67 leden studentlid. Verder telde de vereniging op deze datum 11 corresponderende leden, terwijl vier instituten als begunstigers en vijf donateurs geboekt stonden.

Ook dit jaar werden drie algemene vergaderingen gehouden. Wanneer wij hierbij de chronologische volgorde doorbreken en met de zomervergadering beginnen heeft dit een zeer speciale reden. Het was immers op deze zomervergadering, dat voor het eerst in de geschiedenis van onze vereniging een officieel en bijzonder prettig contact plaats vond met onze Belgische zustervereniging, de „Société Royale de botanique de Belgique". Het initiatief hiertoe was uitgegaan van de voorzitter van de „Société Royale" de Heer C. Van den Berghen uit Brussel. De vergadering vond plaats zaterdag en zondag 1 en 2 september te Oisterwijk. Aan de vergadering en excursies werd deelgenomen door 15 Belgische en 31 Nederlandse deelnemers. De zaterdag was gewijd aan excursies door de Oisterwijkse vennen en het natuurreservaat Kampina, waarbij wij de vereniging tot behoud van natuurmonumenten bijzonder dankbaar mochten zijn voor haar toestemming het gebied van het Beerzedal te mogen bezoeken. De zondag werd besteed aan een excursie op Belgisch grondgebied: een veengebied bij Postel-Arendonck, de Liereman en een veenplas ten Noorden van Turnhout. De Nederlandse excursie stond onder leiding van Dr. V. Westhoff, Dr. J. Th. Reichgelt en J. van Dijk met medewerking van de opzichter van Kampina de Heer J. Beye. De Belgische excursie werd geleid door de Heer C. Van den Berghen. Zaterdagavond werd na een gezamenlijk diner een vergadering gehouden, waarop Dr. J. Heimans iets vertelde over zijn jarenlange onderzoekingen van *„De Desmidiaceae der Oisterwijkse vennen"*, de Heer R. Vanhoorne enkele mededelingen deed over *„Het pollenanalytisch onderzoek der Belgische veengebieden"* en Dr. A. Lawalrée namens de Heer C. Van den Berghen, die die avond verhinderd was aanwezig te zijn, een inleiding hield op de excursie van zondag. De prettige geest, het goede contact tussen de leden van beide verenigingen en de grote belangstelling voor vergadering en excursies wettigden de hoop, dat gecombineerde vergaderingen als deze niet tot één keer beperkt zullen blijven.

Ook de beide andere vergaderingen verheugden zich in een grote belangstelling. De belangstelling voor de jaarvergadering was zelfs uitzonderlijk hoog, doch deze belangstelling gold wel speciaal de bijzondere bestuursverkiezing: het uitzonderlijke feit deed zich namelijk voor, dat de wetenschappelijke vergadering 's middags minder goed bezet was dan de huishoudelijke 's morgens. Op deze wetenschappelijke vergadering spraken Dr. H. T. Waterbolk over: *„Ontstaan en uitbreiding der Angiospermen in het licht van palynologische gegevens"* en Dr. L. C. P. Kerling over *„Eisen, die parasitische schimmels aan hun waardplanten stellen"*.

De oktobervergadering werd gehouden op zaterdag 20 oktober te Utrecht en droeg wederom het karakter van een symposium. Als onderwerp van dit symposium was gekozen: *„De verhouding tussen de bodem en de plant"*. Deze verhoudingen werden belicht van fysiologisch, bodemkundig en biosociologisch standpunt in resp. de voordrachten van Dr. R. Brouwer over *„De invloed van het wortelmilieu op de groei en de opname"*, Dr. A. C. Schuffelen over *„De bodem als milieu voor de plantenwortel"* en Dr. D. M. de Vries over *„De invloed van de bodem op de samenstelling van de vegetatie"*. De grote belangstelling ook voor dit symposium en de levendige discussie toonden, dat het organiseren van symposia in de smaak valt en het bestuur stelt zich voor de najaarsvergadering voortaan steeds zo mogelijk het karakter van een symposium te geven.

Ook de commissievergaderingen werden steeds goed bezocht.

De finantiële toestand van de vereniging geeft gelukkig geen aanleiding meer tot pessimistische beschouwingen, maar voorzichtigheid blijft geboden. Het is daarom, dat we ook thans weer met grote dankbaarheid de subsidies willen vermelden. De subsidie van het departement van onderwijs, kunsten en wetenschappen ten behoeve van de uitgave van de Acta werd dit jaar beëindigd, doch de organisatie voor zuiver wetenschappelijk onderzoek, Z.W.O., stelde ons voor 1956 een subsidie van *f* 4000,- in het vooruitzicht in het kader van de subsidiëring van wetenschappelijke tijdschriften door deze organisatie. Met grote dankbaarheid denken wij ook thans weer aan de giften van onze begunstigers en donateurs. Helaas moeten wij constateren, dat de oproep in het vorige jaarverslag om meer begunstigers en donateurs te winnen, geen gehoor heeft gevonden.

Ook dit jaar verstrekte de Organisatie voor zuiver wetenschappelijk onderzoek ons weer de middelen de secretaris van de „Flora Neerlandica" te salariëren. Het plan bestond, en bestaat nog, dat deze secretaris aan het Rijksherbarium verbonden en dan verder door het Rijk bezoldigd zal worden. Hoewel de definitieve toezegging hiertoe ontvangen was en op grond hiervan geen nieuwe subsidie bij Z.W.O. was aangevraagd, heeft de personeelsstop bij het Rijk de aanstelling van de secretaris onmogelijk gemaakt. Wij zijn de organisatie Z.W.O. zeer erkentelijk voor het feit, dat zij heeft toegezegd zijn salariëring alsnog gedurende zes maanden te willen continueren en wij hopen zeer, dat alsdan de aanstelling door het Rijk weer mogelijk zal zijn.

Dankzij de genoemde subsidies kon de uitgave van de Acta dit jaar gewoon doorgaan. Dat de afleveringen trager verschenen dan vorige jaren en minder goed gevuld waren berustte dan ook niet op gebrek aan geldmiddelen, doch aan gebrek aan kopie. Na de goede kopievoorziening in de voorafgaande jaren is niet aan te nemen, dat we hier in het algemeen met een te geringe produktie aan wetenschappelijke artikelen door de Nederlandse botanici te maken zouden hebben. Waar het vroeger wel voorkwam, dat er een overvloed aan kopie was lijkt het aannemelijker het huidige tekort aan een toevallige fluctuatie te wijten. Het is zeer te hopen, dat de komende jaargang weer beter gevuld zal zijn, temeer waar het aantal betalende abonné's op verheugende wijze gestegen is tot 161.

Het werk aan de „Flora Neerlandica" maakt goede vorderingen. Dit jaar kon een nieuwe aflevering over de Cyperaceae het licht zien. Wij hopen, dat binnen afzienbare tijd de nog restende delen over de Monocotylen afgesloten kunnen worden. Het is zeer verheugend, dat ook voor de Flora van buitenlandse zijde belangstelling bestaat, zodat herhaaldelijk bestellingen voor de reeds verschenen delen binnen komen.

Nog steeds blijft het probleem bestaan, dat de huidige publikatiemogelijkheden, die onze vereniging biedt, niet voldoende blijken te zijn om aan alle verlangens der leden tegemoet te komen. Er kan geen twijfel aan bestaan, dat de moeilijkheden rond de voorzittersverkiezing in januari en februari veroorzaakt waren door het verlangen van bepaalde groepen in de vereniging tot reorganisatie van het tijdschrift. Deze groepen, i. c. de floristen, systematici en biosociologen, hadden reeds enkele jaren wensen naar voren gebracht, doch door onvoorziene omstandigheden moesten de vergaderingen hierover tot tweemaal toe worden uitgesteld. Alvorens opnieuw een vergadering over deze wensen te beleggen achtte het bestuur het beter eerst aan personen uit deze groepen te vragen hun wensen te concretiseren tot een uitvoerbaar geacht plan, opdat een eventuele latere vergadering zich zou kunnen beperken tot de bespreking van de wenselijkheid een dergelijk plan uit te voeren. Onder voorzitterschap van Prof. Dr. S.E. de Jongh is toen een kleine commissie benoemd bestaande uit de leden: Dr. S.E. de Jongh, Dr. F.A. Stafleu, Dr. V. Westhoff en Dr. A. Gorter. Deze commissie kreeg als opdracht zich grondig op de hoogte te stellen van de wensen, die er op het gebied van de publikatiemogelijkheid in de vereniging leven, deze wensen te toetsen aan de finantiele mogelijkheden en eventueel nieuwe finantiele hulpbronnen te suggereren en ten slotte op grond van deze gegevens een of meer plannen te maken, die finantieel uitvoerbaar en voor alle groepen in de vereniging aanvaardbaar geacht konden worden. Het is het bestuur bekend, dat deze commissie zich met grote ijver van haar taak heeft gekweten. Tegen het eind van het jaar was de commissie zover gevorderd, dat het raadzaam leek eerst op ruimere schaal de mening te vernemen over bepaalde aspecten van haar plannen. Het bestuur heeft toen aan de commissie gevraagd een interimrapport op te stellen om dit op ruime schaal door alle belanghebbende groepen in de vereniging te laten bespreken. Dit rapport dat eind 1956 nog niet was verzonden valt buiten de opzet van dit jaarverslag.

Wel mag hier de hoop worden uitgesproken, dat het werk van deze commissie ertoe zal bijdragen, een oplossing te vinden, die voor allen in de vereniging in gelijke mate aanvaardbaar en bevredigend is. Zeer zeker zullen nog vele discussies nodig zijn om een dergelijke oplossing te bereiken, doch reeds thans kan met vertrouwen worden verwacht, dat door het werk van deze commissie een basis gelegd is, die een vruchtbare discussie mogelijk maakt. Laten wij hopen, dat op deze wijze een einde gemaakt kan worden aan een meningsverschil, dat in de aanvang van het jaar zelfs tot een door niemand gewenste tegenstelling in de vereniging dreigde te leiden.

Amsterdam
31 december 1956

De eerste secretaris
A. Quispel

VERSLAG VAN DE COMMISSIE VAN REDACTIE VAN DE ACTA BOTANICA NEERLANDICA OVER 1956

In de samenstelling van de commissie ontstond een wijziging doordat de voorzitter van het bestuur, tevens voorzitter van de commissie van redactie, aan het begin van het verslagjaar aftrad en niet herkiesbaar was. De vereniging is Dr. van Slogteren veel dank verschuldigd voor de wijze, waarop hij steeds de belangen van ons tijdschrift behartigde en naar middelen zocht om te komen tot uitbreiding van het aantal abonnementen, tot grotere toevloed van kopie en vooral tot het verkrijgen van finantiele steun door het werven van donateurs en begunstigers en het ontplooien van grote activiteit ten einde subsidies voor ons werk te verwerven. De commissie is Dr. van Slogteren dankbaar voor de wijze, waarop hij de vergaderingen wist te leiden.

Het periodiek aftredende lid van de Commissie, Dr. S. J. van Ooststroom werd herkozen. Inplaats van Dr. van Slogteren trad de nieuwe voorzitter van het bestuur, Dr. J. Lanjouw op als voorzitter van de commissie. Tijdens de afwezigheid van de secretaris, gedurende de eerste drie maanden van het verslagjaar, was Dr. F. A. Stafleu zo vriendelijk zijn werkzaamheden waar te nemen. De commissie is Dr. Stafleu zeer erkentelijk voor het vele door hem verrichte werk.

De commissie vergaderde gedurende het verslagjaar slechts één maal. Een aantal commissieleden was echter voortdurend betrokken bij de beoordeling van de ingezonden kopie. Speciaal dient hier genoemd te worden het vele werk, dat het commissielid Dr. C. E. B. Bremekamp ook gedurende dit verslagjaar verrichtte: niet alleen beoordeelde hij mede een aantal artikelen maar, evenals vorige jaren, verrichtte hij op voortreffelijke wijze, dikwijls in overleg met de auteurs, de taalkundige correctie van de ingezonden kopie.

De schaarste aan kopie, die tegen het eind van het vorig verslagjaar intrad en waarvan in het vorig jaarverslag reeds sprake was, heeft inderdaad, zoals het vorig jaarverslag reeds aankondigde, een vertragende invloed gehad op het verschijnen van de eerste aflevering, die pas eind mei verscheen. Het was toen mogelijk de tweede aflevering in augustus te laten verschijnen, zodat gehoopt mocht worden dat de volgende afleveringen op tijd zouden afgeleverd worden. Door een langzame gang van zaken op de drukkerij was echter aflevering 3 pas eind november gereed. Op het eind van dit verslagjaar is echter aflevering 4 gereed voor afdrukken. De kopievoorziening laat echter nog te wensen over, zodat in het komende jaar vertragingen in het verschijnen niet uitgesloten geacht moeten worden.

Vol. V werd afgesloten met 354 pagina's tekst, gevolgd door het register, dus aanmerkelijk minder dan de vier voorgaande delen. Deze 354 pagina's zijn verdeeld over 28 artikelen. Het geringere aantal pagina's is een gevolg van de verminderde toevloed van kopie, maar ook van het feit dat het vorig jaar vijf afleveringen verschenen zijn en bovendien is slechts één van de 28 artikelen een dissertatie.

Utrecht
30 december 1956

De secretaris
F. P. Jonker

VERSLAG VAN DE COMMISSIE VOOR HET HERBARIUM, DE BIBLIOTHEEK EN HET ARCHIEF VAN DE KON. NED. BOTANISCHE VERENIGING OVER 1956

In mei 1956 werd het herbarium te zamen met de Nederlandse collectie van het Rijksherbarium overgebracht naar het nieuwe gebouw in de Hortus te Leiden. De door plaatsgebrek nog niet in het herbarium opgenomen planten konden nu door de amanuensis Hendriksen alle worden geïnsereerd. Tegelijk met het herbarium werden ook de Nederlandse en Europese flora's uit de bibliotheek overgebracht naar de bibliotheekkamer van het nieuwe gebouw. Zowel het herbarium als het overgebrachte deel van de bibliotheek inclusief het op de Nederlandse floristiek betrekking hebbende kaartsysteem zijn nu voor de leden van de staf van het Rijksherbarium, die zich met de studie der Nederlandse flora en meer speciaal met werk aan de Flora Neerlandica bezighouden, zeer gemakkelijk te raadplegen.

Het herbarium werd verrijkt met een 7-tal Phanerogamae, geschonken door Dr. E. T. Drion te 's-Gravenhage. Uitgeleend werden 810 exemplaren; niet vermeld zijn hierbij de talrijke nummers, die door leden van de staf van het Rijksherbarium voor hun werk aan de Nederlandse flora werden onderzocht; het totaal aantal uitgeleende exemplaren bedroeg op 31 december van het verslagjaar 948 exemplaren.

Uit de Bibliotheek werden in het verslagjaar 1346 nummers uitgeleend. Aan boeken en overdrukken werden ontvangen 131 nummers, aan tijdschrift-afleveringen 810 exemplaren. Bij de ten geschenke ontvangen publikaties bevinden zich o.a. 60 nummers geschonken door de leden Van Soest en De Langhe en door de Biological Research Group, Utrecht, het Instituut voor Plantenziektenkundig Onderzoek, Wageningen, het Laboratorium voor Tuinbouwplantenteelt, Wageningen, het Staatsbosbeheer te Utrecht en de University of Oxford. Nieuwe tijdschriftseries, die ten geschenke werden ontvangen zijn Coolia, het Correspondentieblad ten dienste van de floristiek en het vegetatieonderzoek van Nederland en Muelleria.

In het Archief werden diverse stukken opgenomen, die werden ingezonden door de penningmeester en de 2e secretaresse.

J.G. Sloff, die aan de beurt van aftreden was als lid der commissie, werd op de jaarvergadering herkozen.

Leiden
1 januari 1957

De secretaris
S.J. van Ooststroom

VERSLAG VAN DE COMMISSIE VOOR HET FLORISTISCH ONDERZOEK VAN NEDERLAND OVER 1956

De Paas- en de Kerstvergadering werden beide gehouden te Amsterdam, op resp. 4 april en 28 december. Als steeds werden beide vergaderingen weer druk bezocht. Op de Paasvergadering werden de volgende voordrachten gehouden: Dr. S.J. van Ooststroom over *„Aanwinsten der Nederlandse flora in 1955"*; Dr. D. Bakker over de *„Senecio aquaticusgroep"*; H.H. Prell over *„Nederlandse adventieven"* en over *„Agropyronsoorten"*; C. den Hartog over *„Nieuwe vondsten van Wieren in Nederland"*; Th.J. Reichgelt over *„De in Nederland adventieve Diplachnesoorten"* en over *„Carex lasiocarpa x riparia in Nederland"*; E.W. Clason over *„Potamogeton lucens x praelongus in Nederland"*; Dr. G. Kruseman over *„Nederlandse Populus-soorten"*.

Op de Kerstvergadering de volgende voordrachten: E.W. Clason over *„De voortzetting van het Drentse District in Duitsland"*; Dr. Th.J. Stomps over *„Een nieuwe mutant van Oenothera biennis"*; Dr. D. Bakker over *„Tussenvormen van Scirpus lacustris ssp. lacustris, id. ssp. glaucus en Scirpus triqueter"*; Dr. S.J. van Ooststroom over *„Aanwinsten der Nederlandse flora in 1956"*; H.H. Prell over *„Diverse adventieven en over Agropyron-bastaarden"*; C. Sipkes over *„Een nieuwe vondst van Ceterach officinarum"*; tevens werd door deze spreker een film vertoond over bloembestuivers.

De zomerexcursie, waaraan 19 leden deelnamen, werd gehouden van 20 tot en met 25 augustus naar Schiermonnikoog, en stond onder leiding van Th.J. Reichgelt. Als merkwaardige vondsten kunnen o.a. worden vermeld *Listera cordata*, nieuw voor het eiland en *Lycopodium annotinus*, nieuw voor de Waddeneilanden.

Ir. J.L. van Soest, die aan de beurt van aftreden was als lid der commissie, werd op de jaarvergadering herkozen.

Leiden
1 januari 1957

De secretaris
S.J. van Ooststroom

VERSLAG VAN DE COMMISSIE VOOR DE BESCHERMING VAN DE WILDE FLORA OVER 1956

Ook in 1956 ontving de commissie van de Directeur van het Staatsbosbeheer enkele rapporten, uitgebracht door de afdeling Natuurbescherming en Landschap van die dienst, over het voorkomen van zeldzame planten in Nederland. Vermelding verdient het rapport betreffende de verspreiding en bescherming van het geslacht *Isoëtes* in Nederland. Nagegaan zal worden in hoeverre de particuliere natuurbeschermingsorganisaties steun kunnen verlenen bij een verdere bescherming van de twee zeldzame soorten van dit geslacht.

Het lid der commissie, Dr. V. Westhoff, stelde ten behoeve van zijn publikatie over de verarming van flora en vegetatie in het Gedenkboek van de Vereeniging tot Behoud van Natuurmonumenten in Nederland „Vijftig jaar natuurbescherming in Nederland" een in verschillende categorieën verdeelde lijst samen van de plantensoorten, die in Nederland zeldzaam zijn en met verdere achteruitgang worden bedreigd. Het ligt in de bedoeling in samenwerking met het Rijksherbarium en het pas opgerichte Rijksinstituut voor Veldbiologisch Onderzoek ten behoeve van het Natuurbehoud te komen tot een verdere uitwerking van deze lijst, hetgeen vooral ook van belang is in verband met het feit, dat bescherming van zeldzame plantensoorten uit hoofde van een Natuurbeschermingswet slechts mogelijk is, wanneer volledige gegevens over de achteruitgang en de huidige verspreiding van deze soorten ter beschikking staan.

Amsterdam
1 januari 1957

De secretaris
R.J. de Wit

VERSLAG VAN DE COMMISSIE VOOR DE FYTOPATHOLOGIE OVER 1956

In de vacature ontstaan door het periodiek aftreden van Dr. D. Mulder werd voorzien door benoeming van Dr. D. Noordam, die het secretariaat waarnam.

Er werden dit jaar twee vergaderingen gehouden. De eerste op vrijdag 4 mei te Utrecht waar Ir. D.H.M. van Slogteren sprak over *„Serologische analyse van enkele plantaardige virussen met behulp van de gel-diffusie methode volgens OUCHTERLONY"*; en Dr. J.P.H. van der Want over *„Nieuwe inzichten in virus vermeerdering bij planten"*. Op de tweede vergadering, vrijdag 9 november te Amsterdam, is een symposium gehouden over het contact tussen plant en parasiet, met het volgende programma:

Dr. A. J. P. Oort, *„Inleiding"*; Dr. A. Jaarsveld, *„De anatomie van de infectie"*; Dr. P. A. Roelofsen, *„De ultramicroscopische structuur van de celwand"*; Dr. O. M. van Andel, *„Opname en verwerking van voedingsstoffen door de parasiet"*; Dr. W. H. Arisz, *„Het transport van stoffen van cel tot cel"*; Dr. A. J. P. Oort, *„Samenvatting"*.

Wageningen
1 januari 1957

De secretaris
Dr. D. Noordam

VERSLAG VAN DE COMMISSIE VOOR DE BIOSOCIOLOGIE EN HET VEEONDERZOEK VAN NEDERLAND OVER 1956

In de samenstelling van de commissie ontstond een wijziging door het aftreden en niet herkiesbaar zijn van Dr. M. F. Mörzer Bruyns, Dr. H. J. Venema en Dr. W. van Zeist; in hun plaats werden tot commissieleden gekozen Dr. F. Florschütz, Dr. D. M. de Vries en Dr. V. Westhoff. Tijdens de afwezigheid van de secretaris gedurende het begin van het verslagjaar werd het secretariaat van de commissie waargenomen door het commissielid Dr. H. T. Waterbolk.

In het verslagjaar organiseerde de commissie twee bijeenkomsten, de 37e en 38e Nederlandse dag voor biosociologie en palaeobotanie.

De 37e dag werd gehouden op 5 april in de collegezaal van het geologisch-mineralogisch instituut van de Rijksuniversiteit te Utrecht. De volgende voordrachten werden gehouden:
Ir. J. H. A. Boerboom uit Wageningen over *„Zonatie en overspoeling van halophyten op de Bosplaat (Terschelling)"*; Dr. V. Westhoff uit Wageningen over *„De ethologische synoecologie van de xero-serie op Terschelling"*; W. H. Zagwijn uit Haarlem over *„Aspecten van de vegetatie bij de overgang van het Plioceen naar het Pleistoceen"* en Ir. F. Maas uit Wageningen over de *„Samenstelling en synoecologie van bronvegetaties"*.

De 38e dag werd gehouden in het botanisch laboratorium van de Rijksuniversiteit te Utrecht op 22 december 1956. Sprekers waren: P. Kuiper (Wageningen) over *„Verlandingsvegetaties in de moerasgebieden van N. W. Overijsel"*; Dr. D. M. de Vries (Wageningen) over *„Indicatie door graslandplanten"*; Ir. W. G. Beeftink (Goes) over *„De halophiele vegetatie van Skallingen (Denemarken"*; B. Zwart Jr. (Amsterdam) over *„Enkele gegevens over het veen op grote diepte onder Amsterdam"*; W. A. E. Donselaar-Ten Bokkel Huinink (Utrecht) over *„Successieonderzoek van moerasvegetaties door analyse van plantenresten in de bodem"* en J. J. Barkman (Leiden) over *„De begrippen vitaliteit, fertiliteit en trouw in de vegetatiekunde"*.

Utrecht
1 januari 1957

De secretaris
Dr. F. P. Jonker

VERSLAG VAN DE COMMISSIE VOOR DE PLANTENFYSIOLOGIE OVER 1956

Op de jaarvergadering werd in plaats van Dr. A. Quispel, die aan de beurt van aftreden en niet herkiesbaar was, benoemd Dr. L. Algera. De functie van secretaris ging daarna op ondergetekende over.

De eerste vergadering in dit jaar werd gehouden op zaterdag 12 mei in het botanisch laboratorium te Utrecht. In de ochtendvergadering hebben gesproken:
Dr. R. Brouwer over *„Onderzoekingen over de passieve en actieve componenten van de ionenopname bij Vicia faba"*; R. N. van Lookeren Campagne over *„Actiespectrum van de lichtinvloed op de absorptie van chloride door Vallisneria"*; en Dr. W. H. Arisz over *„De invloed van licht en suiker op de opname en het transport van chloride bij Vallisneria"*; na de lunchpauze: Mej. Dr. J. Ruinen over *„Beschouwingen over de phyllosfeer"*; Dr. L. K. Wiersum over *„Enkele latex-problemen"*; en Dr. M. J. Adriani over *„Enkele opmerkingen over de waterbalans van halophyten, in het bijzonder die van enige Salicornia-soorten"*.

De tweede vergadering werd gehouden in de collegezaal van het botanisch laboratorium van de Vrije Universiteit te Amsterdam op zaterdag 1 december. Het woord is gevoerd door:
J. Bruinsma over *„Onderzoekingen over de stofwisseling in bladeren en bladcoupes van Bryophyllum tubiflorum"*; Dr. R. van der Veen over *„Beschouwingen over groeistofactiviteit van verschillende phenoxy-azijnzuren en benzoëzuren"*; Ir. L. H. J. Bongers over *„Enige aspekten van de stikstof-assimilatie door algen-kulturen"*; en Dr. J. B. Thomas over *„Photosynthese van chloroplast-fragmenten"* (met film).

Utrecht
1 januari 1957

De secretaris
H. P. Bottelier

VERSLAG VAN DE COMMISSIE VOOR DE PLANTENSYSTEMATIEK EN PLANTENGEOGRAFIE OVER 1956

In verband met het aftreden van Dr. H. J. Venema, die in 1955 voorzitter was en niet herkiesbaar, werd Dr. H. C. D. de Wit tot lid van de commissie benoemd. Voorzitter in 1956 was Dr. R. van der Wijk.

De commissie hield in het afgelopen jaar twee vergaderingen, van welke de eerste werd gehouden op 21 april in het botanisch laboratorium te Utrecht. Voordrachten werden gehouden door:

Dr. H.J.Venema over *„Het Nederlandse kwekerssortiment van het geslacht Helenium"*; Dr. R.van der Wijk over *„Distich en pseudodistich"*; Dr. F.A.Stafleu over *„Het conserveren en verwerpen van namen"*; K.U.Kramer vertelde *„Iets over het genus Lindsaea"* en Dr. H.C.D.de Wit vertoonde *„Een dozijn plantenfoto's uit West-Afrika"*. De vergadering werd bezocht door 29 leden.

De tweede vergadering werd op 27 oktober in Amsterdam gehouden in het Hugo de Vries-laboratorium. Op deze vergadering, die bezocht werd door 32 leden en 2 gasten, spraken de volgende leden:

Dr. F.P.Jonker over *„Het genus Rhizophora in Suriname"*; Dr. B.K.Boom over *„De merkenwet en de botanische nomenclatuur"* en Dr. P.van Royen over *„Het geslacht Batis in Nieuw-Guinea"*. Ir. L.Bos, die als gast aanwezig was, sprak over *„Teratologische verschijnselen bij Tropaeolum"*; Dr. C.G.G.J.van Steenis vertoonde foto's van *„Een botanische reis door Ceylon"* en gaf hierbij toelichtingen.

Leiden
31 december 1956

De wnd. secretaris
J.Th.Koster

VERSLAG VAN DE COMMISSIE TOT HET NAZIEN VAN REKENING EN VERANTWOORDING EN DE BESCHEIDEN VAN DE PENNINGMEESTER OVER 1956

Ondergetekenden, benoemd tot leden van de Kascommissie op de j.l. gehouden jaarvergadering, verklaren hierbij, dat zij op 14 juni ten huize van de penningmeester de boeken en bescheiden van de penningmeester hebben nagezien en gecontroleerd en in orde hebben bevonden.

Zij stellen aan het bestuur voor de penningmeester over het boekjaar 1956 décharge te verlenen. Zij menen, dat de penningmeester grote dank toekomt voor het zorgvuldig beheer en het vele werk door hem voor de Vereniging verricht.

Zij zouden bovendien het volgende onder de aandacht willen brengen. In vergelijking tot het bedrag „crediteuren" (ongeveer ƒ 20.000) is de hoeveelheid kasmiddelen van de Vereniging (ongeveer ƒ 50.000) groot. Deze middelen brengen slechts een zeer bescheiden rente op. Aangezien in de afgelopen twintig jaar de fondsen van de Vereniging niet zijn aangevuld geeft deze gunstige kaspositie de mogelijkheid dit alsnog te doen. Het constant houden van de fondsen heeft geleid tot een feitelijke waardevermindering in verband met de waardedaling van de gulden.

Het is bovendien aan ondergetekenden opgevallen dat de versterking van de kaspositie van het Vrije Fonds onder anderen het gevolg is van het op dit fonds boeken van winsten gemaakt op publikaties die grotendeels betaald zijn uit de twee andere fondsen. In verband hiermede zouden zij de volgende suggesties willen doen.

1 de (betrekkelijk bescheiden) kassaldi van het Kok-Ankersmit- en het Brumund Fonds toe te voegen aan het kapitaal van die fondsen door aankoop van effecten.

2 van het (grote) kassaldo van het Vrije Fonds een bedrag ter grootte van 20% van het huidige totaal der drie fondsen toe te voegen aan dat kapitaal door aankoop van effecten en wel in een verhouding overeenkomend met de huidige grootte der drie fondsen.

Utrecht/Leiden
17 juni 1957

F.A.Stafleu
A.G.de Wilde

VERLIES- EN WINSTREKENING OVER 1956

Kok Ankersmit fonds

Overdrachten	575,-	Ontvangsten (interest)	1.419,78
Nadelig saldo Effecten	2.707,08	Saldo verlies	1.862,30
	3.282,08		3.282,08

Brumund fonds

Overdrachten	100,-	Ontvangsten (interest)	772,35
Nadelig saldo Effecten	1.906,23	Saldo verlies	1.233,88
	2.006,23		2.006,23

Vrije fonds

Nadelig saldo koersverschil	1.052,31	Interest	887,18
Vergaderingen	419,15	Contributies (1956 en vorige jaren)	7.857,61
Bibliotheek	485,43	Ned. Kruidk. Archief	9,60
Onkosten	1.171,45	Prodromus	21,-
Lidmaatschappen	269,10	Recueil	494,80
Jaarboek	649,16	Crediteuren	211,11
Debiteuren *)	3.474,59		
Saldo winst	1.960,11		
	9.481,30		9.481,30

*) Specificatie debiteuren

Overdracht Flora Neerlandica	2.232,50
Overdracht Acta Botanica	3.495,73
	5.728,23
Winst debiteuren	2.253,64
	3.474,59

Acta Botanica Neerlandica

Balans 1 januari 1956	4.000,-	Abonnementen	3.248,71
Deel 5 (1 + 2)	6.959,-	Bijdrage Rijk 1955	4.000,-
Crediteuren deel 5 (3 + 4)	7.800,-	18 ex Rijk	450,-
		Debiteuren	1.225,75
		Overdrukken, enz.	2.188,81
		Bijdragen instituten	2.750,-
		Bijdragen industrie	1.400,-
		Overdracht	3.495,73
	18.759,-		18.759,-

Flora Neerlandica

Crediteuren	3.250,-	Verkoop	950,30
		Overdracht	2.232,50
		Debiteuren (nog te vorderen	67,20
	3.250,-		3.250,-

BALANS, 31 DECEMBER 1956

Kok Ankersmit fonds

Effecten	44.464,-	Fonds per 1 januari 1956	40.103,99
Kasgeld	4.069,71	Aflossing hypotheek	10.516,16
Interest	224,14		
Saldo verlies	1.862,30		
	50.620,15		50.620,15

Brumund fonds

Effecten	17.563,22	Fonds per 1 januari 1956	27.100,71
Kasgeld	8.008,81	Claim	75,-
Interest	369,80		
Saldo verlies	1.233,88		
	27.175,71		27.175,71

Vrije fonds

Effecten	8.953,-	Fonds per 1 januari 1956	27.761,07
Kassaldo	40.196,33	Contributie 1957	649,55
Contributie (nog te vorderen 1956)	830,-	Crediteuren	21.788,33
Interest	560,98	Saldo winst	1.960,11
Debiteuren	1.618,75		
	52.159,06		52.159,06

BEGROTING 1957

Kok Ankersmit fonds

Inkomsten	1.400,-	Herbarium, bibliotheek en archief	500,-
		Flora Neerlandica	770,-
		Natuurmonumenten en Wahlenbergia terr.	105,-
		Onkosten	25,-
	1.400,-		1.400,-

Brumund fonds

Inkomsten	750,-	Flora Neerlandica	600,-
		Commissies	100,-
		IVON	25,-
		Onkosten	25,-
	750,-		750,-

Vrije fonds

Interest	800,-	Vergaderingen	450,-
Contributies	8.000,-	Acta Botanica	5.600,-
		Flora Neerlandica	600,-
		Jaarboek	700,-
		Commissies	40,-
		Lidmaatschappen	194,-
		Onkosten	1.200,-
		Onvoorzien	16,-
	8.800,-		8.800,-

Acta Botanica Neerlandica

Vrije fonds	5.600,-	Uitgave deel 6	18.000,-
ZWO	4.000,-	Onkosten	200,-
Instituten	3.000,-		
Industrie	1.900,-		
Verkoop	3.700,-		
	18.200,-		18.200,-

Flora Neerlandica

Kok Ankersmit fonds	770,-	Uitgave	3.400,-
Brumund fonds	600,-	Onkosten	70,-
Vrije fonds	600,-		
Verkoop	1.500,-		
	3.470,-		3.470,-

NOTULEN VAN DE JAARVERGADERING, GEHOUDEN IN HET HUGO DE VRIES-LABORATORIUM TE AMSTERDAM OP ZONDAG 26 FEBRUARI 1956

De voorzitter Dr. E. van Slogteren opent om 10.45 uur de vergadering. Aanwezig zijn 79 leden nl.: Arisz, von Arx, von Arx-van der Brugge, Bakhuizen van de Brink, Barkman, Bas, Beijer, A. J. Bianchi, F. Bianchi, Bottelier, Bruinsma, le Consquino de Bussy, Doing Kraft, Donk, van Eyndhoven, P. A. Florschütz, Fuchs, Gorter, Groenhart, Groenhuijzen, van Hattum, van Heel, Hegnauer, Heimans, Hekking, van Herk, Hille Ris Lambers, Jaarsveld, Jensma, S. E. de Jongh, Kamerbeek, Karstens, Kerling, Kern, Koningsberger, J. Th. Koster, Kramer, G. Kruseman Jr., Lam, Lanjouw, van Leeuwen, Leeuwenberg, J. C. Lindeman, Löhnis, R. A. Maas Geesteranus, A. Mennega, Niekerk-Blom, van Nigtevecht, Reinders, Reinders-Gouwentak, van Ooststroom, Prell, van der Pijl, Quispel, Reichgelt, de Roon, Schimmel, D. H. M. van Slogteren, E. van Slogteren, Slootweg, Smeets, van Soest, Spierenburg, Stafleu, Stegwee, Stomps, Thomas, P. Vermeulen, van der Voo, Waterbolk, Westhoff, Weurman, de Wilde, van der Wijk, de Zeeuw, F. Zeijlemaker, twee onleesbaar en drie introducé's, nl. Kanis, Touw en Zwart.

De voorzitter herdenkt de leden, die in het afgelopen jaar de vereniging door de dood zijn ontvallen, de beide ereleden Jansen en Pulle en Dr. G. Stahel.

Vervolgens worden de notulen van de algemene ledenvergadering, gehouden te Amsterdam op zaterdag 8 oktober 1955 voorgelezen en goedgekeurd.

Daarna brengt de eerste secretaris zijn verslag uit over het jaar 1955.

De ontwerp-jaarverslagen van de Permanente Commissies worden hierna voorgelezen en alle goedgekeurd; de voorzitter dankt alle secretarissen voor hun werk. Van de subcommissie voor het Zuiderzee-onderzoek is geen verslag ontvangen.

De penningmeester begint daarna zijn verslag over het jaar 1955 met een bespreking van de Winst- en Verliesrekening. Daarna bespreekt hij de Balans en geeft een overzicht over het financiële beheer van de Acta bot. .neerl. Nadat de penningmeester op enkele gevraagde informaties geantwoord heeft gaat hij over tot een bespreking van de begroting, ook voor de uitgave van de Acta bot. neerl. en van de Flora neerl. De begroting wordt hierna aangenomen en de voorzitter dankt de penningmeester voor het vele werk, dat hij ook dit jaar weer voor de vereniging verricht heeft bij het zorgvuldig beheren van de financiën.

Tot leden van de Commissie tot nazien van de rekening en verantwoording en de bescheiden van de Penningmeester over 1955 worden benoemd de leden P. Vermeulen en A.G. de Wilde, van welke de laatste zich bij het bespreken van de begroting als een goed rekenaar liet kennen. Beide aanvaarden de benoeming.

De candidaatleden per convocatie voorgesteld (en van wie aanwezig zijn Kanis, Touw en Zwart) worden alle bij acclamatie benoemd, evenals 10 leden, die met dispensatie van artikel 6, 1e lid der statuten staande de vergadering worden voorgesteld (T.W.J. Gadella, A. Haandrikman, M.T. Jansen, F.M. Maas, H. Passchier, H. Veen, K. Verhoeff, L.IJ.Th. Westra, L.J. de Wit, G.H. Zeilmaker).

In de vacatures voor de Permanente Commissies worden, eveneens bij acclamatie, de leden, die per convocatie zijn voorgesteld, benoemd.

Hierna geeft de voorzitter een kort overzicht over zijn beleid in de afgesloten 5 jaar, speciaal ook wat het tijdschrift, de Acta bot. neerl. aangaat. Zijn opdracht was, te zorgen voor een tijdschrift, dat de publikaties van de leden van de Kon. Ned. Bot. Ver. zou bevatten. En nu is er een tijdschrift, dat ook in het buitenland goed ontvangen wordt, dat bovendien de enige band is, die de zo zeer gespecialiseerde leden van onze vereniging nog bijeenhoudt. Voor dit tijdschrift waarin op internationaal niveau de botanische wetenschap van Nederland gepubliceerd wordt, wordt ook door verschillende industrieën subsidie beschikbaar gesteld. Toch heeft de voorzitter niet volledig kunnen bereiken, dat alle leden bijeen bleven en in verband hiermede zet hij de candidatuur van Dr. Lanjouw, zoals deze op de tweede convocatie is aangekondigd, uiteen.

Dr. Lam merkt op, dat de „floristen" in ieder geval het voortbestaan van de Acta bot. neerl. als zodanig wensen, maar daarnaast een publikatie-mogelijkheid zouden willen zien ter versterking van hun onderlinge band.

In zijn antwoord stelt de voorzitter voor een uitgebreide discussie over de tijdschrift-kwestie uit te stellen tot later.

Hierna wordt tot stemming overgegaan. Aanwezig zijn 81 stemgerechtigde leden, van wie P.A. Florschütz, Dr. Waterbolk en Dr. van der Wijk het stembureau vormen. Uitgebracht worden 54 stemmen op Lanjouw, 24 op Van Herk, 3 blanco; Dr. Lanjouw is tot voorzitter benoemd.

De onder-voorzitter Dr. Van Ooststroom dankt de aftredende voorzitter Dr. E. van Slogteren in een kort woord voor het vele, dat hij voor de Vereniging gedaan heeft en releveert in het bijzonder zijn bemoeiingen op finantiëel gebied, vooral ook voor het verkrijgen van subsidies voor de Acta bot. neerl.

Daarna wordt in het laboratorium een eenvoudige koffiemaaltijd gebruikt.

Om 14 uur wordt de vergadering heropend door de voorzitter Dr. Lanjouw. Twaalf leden, die de ochtendvergadering niet bijwoonden, zijn nu wel aanwezig nl.: Andreas, Belderok, van Beverwijk, de Boer, de Bruin-Brink, Heybroek, Kanis, van Lookeren Campagne, Polak, Roodenburg, Ruinen, Touw. Allereerst bedankt de voorzitter Mevr. Dr. Vos-Simon Thomas voor haar goede zorgen voor de koffiemaaltijd en spreekt een woord van welkom tot Dr. J. Ruinen, die na een verblijf van 10 jaar in Indonesië, in ons land is teruggekeerd.

Daarna verkrijgt Dr. H. T. Waterbolk het woord voor zijn voordracht over: *„Ontstaan en uitbreiding der Angiospermen in het licht van palynologische gegevens"*. Niet alleen in veen, bruinkool en steenkool, doch ook in kleiën, schalies, zout en andere gesteenten blijven pollen en sporen bewaard. Zij zijn dus de meest universele botanische fossielen. Op grond van het thans beschikbare materiaal is het nog niet mogelijk met zekerheid te bepalen waaruit de Angiosperme pollen-typen zijn ontstaan. Mono- en dicotyle typen treden beide zeer vroeg op; in het krijt vindt men tussenvormen met Gymnosperme pollentypen, doch ook met microsporen van Pteridophyten. Na een discussie waaraan deelgenomen wordt door Dr. Reinders-Gouwentak, Dr. Kerling en Dr. Lam, is er een korte theepauze.

Om 15.30 uur vangt Dr. Kerling haar voordracht aan over: *„Eisen, die parasitaire schimmels aan hun waardplanten stellen"*. Wil een samenleving tot stand komen tussen een plant en een parasitaire schimmel, dan moeten de partners potentiëel bij elkaar passen, terwijl bovendien de omstandigheden daartoe gunstig moeten zijn. Voor het tot stand komen van een dergelijke verhouding, zoals tussen bepaalde tarwe-variëteiten enerzijds en meeldauw of roesten anderzijds, die genetisch zeer nauw op elkaar afgesteld zijn, schijnen de omstandigheden jaarlijks gedurende kortere of langere tijd gunstig te zijn. Deze schimmels behouden gedurende hun gehele levenscyclus een biotroof karakter. Anderen doorlopen, naast een biotroof een necrotroof stadium. Zo voltooit *Venturia inaequalis*, die schurftvlekken op levende appelbladeren veroorzaakt, de levenscyclus in het dode blad, waarin zich de peritheciën ontwikkelen. Niet altijd is een binnengedrongen parasiet makkelijk waar te nemen, daar deze vaak geen uitwendig zichtbare symptomen veroorzaakt. Deze verschijnen soms pas in de vorm van fructificaties van de schimmel, als het weefsel van de waardplant een bepaalde graad van afsterven, of een bepaalde staat van rijping, bereikt heeft. Zo dringt *Colletrotrichum spinaciae* behalve bladeren van spinazie ook bladeren van Chenopodiaceae binnen. Terwijl er snel vlekken op spinaziebladeren zichtbaar worden, ontstaan er pas conidiën op de bietenbladeren als deze door ouderdom vergelen. Schimmels, die zich tijdens de bewaring manifesteren bij appels, zijn waarschijnlijk reeds in de vruchten binnengedrongen, toen deze nog onrijp aan de boom hingen. Zij wachten in latente toestand de gunstige omstandigheden af om tot verdere ontwikkeling te komen.

Weer andere schimmels dringen een plantendeel niet binnen, vóór dat dit in een voor hen gunstige toestand is gekomen. Door cultuur maatregelen, b. v. door extreem vervroegen kan een gewas in een dergelijke toestand van praedispositie gebracht worden. Aan de discussie nemen deel Dr. E. van Slogteren, Dr. Hille Ris Lambers en Dr. Lanjouw.

Om 16.15 uur sluit de voorzitter de vergadering.

20 oktober 1956

De voorzitter
J. Lanjouw

De 2e secretaresse
J. de Zeeuw

NOTULEN VAN DE ZOMERVERGADERING MET EXCURSIES OP ZATERDAG 1 EN ZONDAG 2 SEPTEMBER 1956

Deze zomervergadering en de excursies vonden plaats in samenwerking met de Société de Botanique de Belgique.

Op zaterdag 1 september verzamelden de deelnemers zich in Oisterwijk, vanwaar om 10 uur vertrokken werd van Hotel De Zwaan, om een bezoek te brengen aan de Choorvennen, die voor het publiek toegankelijk zijn.

Na de lunch in „Groot Speyck" bracht de bus ons naar de Kampina, waar een lange wandeling door dit bijzonder mooie en interessante terrein gemaakt werd. Als excursieleiders fungeerden de leden J. van Dijk, Westhoff en Reichgelt.

Na het diner, dat in Hotel de Zwaan plaats vond, opende de voorzitter Dr. Lanjouw om 9.15 uur de vergadering. Aanwezig zijn de leden: Brinkman, E.E. Harmsen, Heimans, Heybroek, Jonker, Lanjouw, Misset, Muller, Oomen, Polak, Quispel, Reichgelt, van Soest, van Steenis, J.J. Swart, Westhoff, Westra, Wildervanck, de Zeeuw, Zeijlemaker en 18 introducé's onder wie 15 Belgen.

In zijn opening releveert de voorzitter dat dit de eerste keer is, dat beide verenigingen samen komen, terwijl er wel eerder individuele contacten zijn geweest. Het initiatief van deze gecombineerde vergadering is uitgegaan van Mr. Van den Berghen, terwijl de beide secretarissen Lawalrée en Quispel en ook de secretaris van de V. V. V. te Oisterwijk de dank van alle deelnemers verdienen voor al het werk dat zij bij het organiseren hebben verricht.

Het huishoudelijk gedeelte is tot een minimum beperkt. Sinds de jaarvergadering is overleden het corresponderend lid Merrill van Harvard University, terwijl het heengaan van Prof. Kluyver in mei 1956 een verlies voor de hele wereld betekent.

Een ogenblik stilte wordt in acht genomen ter herdenking van hen beiden.

De 8 candidaatleden per convocatie voorgesteld worden alle bij acclamatie benoemd, evenals de 2 leden, die met dispensatie van artikel 6, 1e lid der statuten staande de vergadering worden voorgesteld (J.A. Bekkering en E. van Rompay).

Daarna wordt overgegaan tot het wetenschappelijk gedeelte. De eerste spreker op het programma vermeld, M.A. Bodeux, neemt geen deel aan de bijeenkomst, en in zijn plaats leest Dr. Lawalrée de voordracht voor, die Mr. Van den Berghen zou houden over de excursie van zondag, aangezien Mr. Van den Berghen alleen zondag aanwezig zal kunnen zijn. Dr. Lawalrée betuigt zijn dank aan de Hollandse botanici voor hetgeen zij de afgelopen dag hebben getoond en spreekt vervolgens over de vegetatie van de tourbières bij Postel-Arendonck, de Liereman en de Zwarte Vennen, die zondag bezocht zullen worden.

Daarna spreekt Dr. J.Heimans over de Desmidiaceae van de vennen bij Oisterwijk. De spreker noemt eerst de namen van hen, die de stichters zijn geweest van dit Natuurmonument: Thijsse, Perk en Van Tienhoven, en gaat dan over op het hydrobiologisch onderzoek van de vennen; in 1916 is begonnen met een onderzoek naar de zeer rijke Desmidiaceae vegetaties in de verschillende vennen. Merkwaardigerwijs bleken er zeer onverwachte soorten voor te komen, o.a. uit bergmeren van Schotland, Scandinavië en Finland. De Desmidiaceae-vegetaties in de verschillende vennen bleken in die tijd zeer verschillend te zijn. Het bleek onmogelijk na te gaan, welke milieu-component de waargenomen verschillen in vegetatie veroorzaakt heeft. In verband hiermede voerde Heimans de accessibiliteitsfactor in.

Aan de hand van een aantal lantarenplaatjes werden ons een groot aantal Desmidiaceae met hun bijzonderheden getoond.

Kort werd nog ingegaan op het grote verschil in vegetatie tussen het Voorste en het Achterste Choorven.

Wegens tijdgebrek werd geen gelegenheid gegeven tot vragen stellen.

Als derde spreker gaf de Belg Vanhoorne een kort overzicht van de resultaten van het pollenanalytisch onderzoek in de terreinen van de Belgische Kempen, die zondag bezocht zouden worden.

Na de spreker zijn dank betuigd te hebben sluit de voorzitter om ongeveer 11 uur de vergadering.

Zondag 2 september vertrokken de deelnemers om 9.15 uur met 2 bussen en enige particuliere auto's uit Oisterwijk. Onder leiding van Lawalrée werd het gebied bij Postel-Arendonk bezocht, terwijl Van den Berghen daarna de leiding overnam voor het bezoek aan de Liereman en de Zwarte Vennen.

Het geheel was een bijzonder geslaagde excursie, bij voor deze zomer goed weer, door een interessant en mooi terrein, waaraan werd deelgenomen door ongeveer 15 Belgen en 30 leden van de Kon. Ned. Bot. Ver. Om ongeveer half 6 ging de Belgische bus verder België in, en de Hollanders keerden terug over de grens naar Tilburg, waar ieder zijns weegs ging.

20 oktober 1956

De voorzitter
J.Lanjouw

De 2e secretaresse
J.de Zeeuw

NOTULEN VAN DE ALGEMENE LEDENVERGADERING GEHOUDEN TE UTRECHT OP ZATERDAG 20 OKTOBER 1956

Aan het Symposium over de betrekkingen tussen de bodem en de plant, dat om 15.30 uur aanvangt in de grote collegezaal van het Botanisch Laboratorium gaat een korte huishoudelijke vergadering in de kleine collegezaal vooraf.

Om 15.05 uur opent de voorzitter, Dr. Lanjouw, deze huishoudelijke vergadering. De notulen van de jaarvergadering en van de zomervergadering met excursies worden voorgelezen en goedgekeurd. In verband met de décharge van de penningmeester over 1955 leest de eerste secretaris de brief van de leden De Wilde en Vermeulen voor, waarin zij verklaren dat zij op 10 april 1956 de boeken en bescheiden van de penningmeester hebben gecontroleerd en in orde bevonden. Hierna wordt aan de penningmeester décharge over 1955 verleend.

De beide candidaat-leden per convocatie voorgesteld worden bij acclamatie benoemd, evenals vijf leden die met dispensatie van artikel 6, 1e lid der statuten staande de vergadering worden voorgesteld door de leden Arisz, Brouwer en Helder (het zijn: H.J. Baarda, J.H. Bonga, H. van der Heide, G. Jager en Mej. A.G. van der Molen).

In verband met de zomerexcursie merkt de voorzitter nog op, dat misschien het volgend jaar weer een dergelijke gecombineerde excursie gemaakt kan worden.

Wanneer de voorzitter om 15.30 uur in de grote collegezaal het Symposium opent, blijkt evenals vorig jaar uit de grote opkomst de belangstelling voor dit symposium. Een speciale uitnodiging om bij dit symposium aanwezig te zijn was gezonden aan de leden van de Bodemkundige Vereniging en van de Velebi. 55 leden (Alberda, Algera, van Andel, Arisz, Barkman, Becker, Beumée, A.T.J. Bianchi, Brinkman, R. Brouwer, de Bruin-Brink, de Bruyn, Casparé, van Die, Doing Kraft, van Donselaar-ten Bokkel Huinink, J.Z. van Dijk, E.E. Harmsen, Helder, Heijl, Hille Ris Lambers, van der Houven van Oordt-Hulshoff, Jonker, Kanis, Karstens, Lanjouw, Lens, J.C. Lindeman, A.M.W. Mennega, Nieuwdorp, van Nigtevecht, van Ooststroom, Pouwer, Prell, v.d. Pijl, A. Quispel, van Raalte, Reïnders-Gouwentak, E. van Slogteren, van Soest, Sol, Stafleu, Touw, van der Tuin, Uri, v.d. Voo, Vreede, D.M. de Vries, J.C. Went, Westhoff, Wiersum, de Zeeuw, Zeijlemaker en 2 onleesbaar) en 22 introducé's wonen de voordracht bij.

De voorzitter spreekt het woord van welkom en wekt de niet-leden op zich als lid van de Kon. Ned. Bot. Ver. op te geven. Daarna geeft hij het woord aan Dr. R. Brouwer voor zijn voordracht over: *„De invloed van het wortelmilieu op de groei en de opname"*. Wanneer men de invloed van het milieu op de drogestof-productie wil nagaan, is het moeilijk om de werking van één factor b.v. de temperatuur, te bestuderen. Men kan de invloed van één factor op verschillende planten en de invloed van verschillende factoren op één plant onderzoeken.

De volgende factoren spelen een rol bij de groei van het wortelstelsel: water, aëratie, temperatuur, en ionenconcentratie. Aan de hand van diapositieven wordt op het gedrag van deze factoren nader ingegaan, terwijl spreker besluit met de opmerking dat tot nu toe nog veel te weinig onderzoek op dit gebied is verricht.

Om 16.30 uur geeft de voorzitter het woord aan Prof. Schuffelen, die als gast een bijzonder woord van welkom in ontvangst heeft te nemen. De titel van zijn voordracht is: *„De bodem als milieu voor de plantenwortel"*.

Spreker begint zijn voordracht met de bodem in drie fasen te verdelen nl.

1e. een vaste fase, die het anorgan. en organ. deel bevat en het levende gedeelte;
2e. een vloeibare fase dwz.: water en zouten en de opgeloste organische stof;
3e. een gasvormige fase.

De verschillende eigenschappen van de bodem zijn afhankelijk van dit 3-fasensysteem. De eigenschappen kunnen we verdelen in fysische en chemische. Van de fysische eigenschappen worden besproken de temperatuur, O_2- en CO_2-gehalte en water. Van de chemische eigenschappen wordt nader ingegaan op de anionen- en op de kationenconcentratie, waarbij de complicaties, die zich in de bodem kunnen voordoen, worden behandeld.

Hierna wordt de discussie over deze beide voordrachten, die nauw met elkaar verband houden, geopend. Nadat een groot aantal vragen is gesteld, waar geanimeerd op wordt ingegaan, sluit de voorzitter om 17.50 de discussie na beide sprekers van harte bedankt te hebben.

In de nu volgende pauze bestaat gelegenheid tot het nuttigen van zelf meegebrachte boterhammen onder het genot van een kopje koffie.

Om 19 uur vangt Dr. de Vries zijn voordracht aan over: *„De invloed van de bodem op de samenstelling van de vegetatie"*. Spreker ving aan met voorlezing van het uittreksel van de voordracht: *„De samenhang tussen vegetatie en milieu, in het bijzonder de bodem"*, gehouden door Dr. V. Westhoff voor het symposium *„Bodem en vegetatie"*, georganiseerd door de Nederlandse Bodemkundige Vereniging op 7 mei 1954 te Wageningen. Verwezen werd naar de publicatie van deze voordracht van algemene strekking in het T. N. O. nieuws, Jaarg. 10, afl. 1 (jan. 1955), p. 9-16.

Daarna bracht spreker het voornaamste naar voren van de voordracht *„Grasmat en bodem"*, in het kader van genoemd symposium gehouden door hemzelf, mede namens Ir. Th.A.de Boer, welke voordracht niet is gepubliceerd.

Verder werd de voordracht *„Indicatie door graslandplanten"* gevolgd, door spreker op 15 mei 1956 te Wageningen gehouden als onderdeel van de Vacantie-cursus „Grasland".

Werden aldus de voornaamste uitkomsten naar voren gebracht van het eigen, specialistische oecologisch graslandonderzoek, voor zover dit op de bodem betrekking heeft, het slot: een de fysiologie rakende verklaring van de in de plantengeografie ontstane begrippen „minnendheid" en „mijdendheid" van soorten, was weer van algemeen belang. In dit verband zij verwezen naar de samenvatting in dit Jaarboek van de voordracht *„Indicatie door graslandplanten"*, door spreker op 22 december 1956 te Utrecht gehouden voor de 38e Dag voor Biosociologie en Palaeobotanie.

Nadat de spreker nog enkele vragen beantwoord heeft, sluit de voorzitter om 20.15 uur het symposium.

27 januari 1957

De voorzitter
J. Lanjouw

De 2e secretaresse
J. de Zeeuw

KORTE SAMENVATTINGEN VAN ENKELE VOORDRACHTEN, GEHOUDEN IN DE COMMISSIEVERGADERINGEN

COMMISSIE VOOR DE FYTOPATHOLOGIE

Ir. D.H.M. van Slogteren: Serologische analyse van enkele plantaardige virussen met behulp van de gel-diffusie methode volgens OUCHTERLONY.

De serologische gel-diffusie methode volgens Ouchterlony berust erop, dat tussen 2 basins, die in een laag agar zijn geponst of met een metalen matrijs zijn uitgespaard tijdens het gieten, precipitatielijnen ontstaan indien zich in het ene basin een suspensie van antigenen (b.v. eiwitten of weefselextracten) en in het andere antiserum met homologe antilichamen bevinden.

Bij aanwezigheid van verschillende antigenen met ieder hun eigen mate van diffusie, kunnen verschillende precipitatielijnen ontstaan, een differentiatiemogelijkheid, die met andere methoden minder gemakkelijk realiseerbaar is.

Met behulp van deze methode werden in sap van tabaksplanten, besmet met verschillende virusstammen, behorende tot de Cucumisvirus 1-groep (Tomaat-Aspermy virus, Cucumisvirus 1 stam Chrysanth-Noordam, en verder een „gele" en een „groene" stam van dit virus) behalve gemeenschappelijke, ook antigenen aangetoond, die stamspecifiek zijn.

Op analoge wijze kan worden gedifferentieerd tussen virussen van het tabaksnecrose type.

In sap van planten, besmet met tabaksmozaiekvirus kunnen tenminste 2 onafhankelijke antigene componenten worden gedemonstreerd.

Voorlopige resultaten, verkregen met viruszieke anjers wettigen de hoop dat voor dit gewas de methode zich leent voor een eenvoudig routine onderzoek, dat het gebruik van een centrifuge overbodig maakt.

Dr. Ir. J. P. H. van der Want: Nieuwe inzichten in virus vermeerdering bij planten.

In de voordracht werd een overzicht gegeven van wat op verschillende wijze bekend is geworden over vorm en structuur van plantevirussen, in het bijzonder van het tabaksmozaiekvirus (electronenoptisch, met behulp van röntgenanalyse en chemisch). Daarna werd ingegaan op de betekenis van de twee essentiële onderdelen van het virus, nl. eiwit en nucleïnezuur.

Symposium over het contact tussen plant en parasiet.

Mej. Dr. A. Jaarsveld: De anatomie van de infectie.

Schimmel infecties kunnen bij de plant actief plaats vinden, terwijl virussen en bacteriën passief binnenkomen. Zo vormt *Botrytis cinerea* een kiembuis op de cuticula en hecht zich met slijm op deze vast. Daarna dringt de schimmel door de intacte huid binnen. Vermoedelijk vindt het penetreren van de wand mechanisch plaats, gecombineerd met werking van enzymen. Meeldauwschimmels en o.a. *Venturia* en *Diplocarpon* komen evenzo door de cuticula binnen. Door natuurlijke openingen o.a. huidmondjes kunnen ook schimmels binnendringen en dit is ook de weg die door vele bacteriën gevolgd wordt. Een schimmel als *Phytophthora* kan zowel door huidmondjes als door een intacte huid binnendringen. Bacteriën dringen behalve door natuurlijke openingen en wonden ook binnen door plantendelen zonder cuticula zoals worteltoppen, wortelharen, stengels en nectariën. Infectie door virussen vindt plaats door uiterst kleine wonden, waarschijnlijk via plasmodesmen of misschien ook door submicroscopische celwandopeningen. Op plaatsen waar de schimmel binnendringt vindt vaak een verdikken van de celwanden plaats en kernen, ook van naburige cellen die geen contact hebben met de parasiet, begeven zich in de cel in de richting van de parasiet. In omgevende gedesorganiseerde cellen vormt de parasiet nu haustoriën en opname van voedsel vindt plaats.

Dr. P. A. Roelofsen: De ultramicroscopische structuur van de celwand.

In de, ten dele kristallijne, cellulose van de celwand bevinden zich incrustaties van amorf hemicellulose. Pectine bevindt zich in de middenlamel, maar ook in de cellulosewand. Het is de vraag of het amorf of kristallijn is; na oplossen van cellulose is pectine fibrillair aanwezig. Aan de hand van vele electronenmicroscopische afbeeldingen werd de bouw van de celwand verduidelijkt. Een beeld werd zo gegeven voor de verschillende richtingen waarin de cellulosefibrillen liggen en de veranderingen die daarin tijdens de groei plaats vinden. In het bijzonder gaf onderzoek van de laatste jaren waarbij ontelbare openingen in de celwanden werden aangetoond waarin zich plasmodesmata bevinden, de fytopathologen stof tot denken over de rol die de plasmodesmata kunnen spelen bij infecties.

Mej. Dr. O.M. van Andel: Opname en verwerking van voedingsstoffen door de parasiet.

Besproken werd welke elementen als anorganische stoffen voor groei van schimmels aan media dienen te worden toegevoegd. Hiernaast zijn talrijke organische stoffen voor de groei van bepaalde schimmels nodig.

Dr. W.H. Arisz: Het transport van stoffen van cel tot cel.

In een blad heeft naast aan- en afvoer van stoffen door de vaatbundels ook verplaatsing van stoffen plaats van cel tot cel en overgang van stoffen uit parenchymweefsel in vaatbundels en omgekeerd. Zeefvaten zijn als gespecialiseerde parenchymcellen te beschouwen, daarom is het onderzoek van parenchymatisch transport fundamenteel.

De schede van de vaatbundel bestaat uit aaneengesloten parenchymcellen met dunne wanden. Deze begeleiden de vaatbundels tot hun uiteinden en transporteren water en zouten. Dit parenchymatisch transport heeft zeker ten dele door het plasma plaats; in hoeverre de celwanden hierbij een rol spelen is nog niet opgehelderd. Er is plasmatisch contact tussen aangrenzende cellen door plasmaverbindingen en plasmodesmata, zodat eenmaal in het plasma opgenomen stoffen in het symplasma getransporteerd worden zonder naar buiten te worden afgegeven. Het passeren van de grenslagen vereist energie, ook afgifte van stoffen uit het plasma aan de vacuole is met stofwisselingsprocessen verbonden. Schumacher twijfelt aan de betekenis der plasmodesmata voor het transport op grond van het ontbreken van plasmodesmata bij het transport uit de zeefvaten van het gastheerplant naar de haustoriën van *Cuscuta*. Er wordt door de spreker op gewezen, dat dit begrijpelijk is, daar de hyphen tussen de zeefvaten van de gastheerplant indringen, zodat stoffen uit de zeefvaten door de opengelegde zeefplaten van zelf naar buiten komen, waardoor plasmodesmen tussen gastheer en parasiet overbodig zijn. Besproken wordt het verschillend gedrag van zouten en organische stoffen als suikers en aminozuren bij het transport van cel tot cel. Ter sprake komen nieuwe biochemische onderzoekingen van Miss Porter over suikeropname door tabaksbladen met gemerkte koolstof, evenzo onderzoekingen van Wanner over de aanwe-

zigheid van phosphatase in de schedecellen van de vaatbundel. De stofwisseling in de zeefvaten zelf zou gering zijn. Zij vervoeren suikers en phosphaten afzonderlijk doch niet als suikerphosphaten.
Ten slotte wordt op de betekenis van het onderzoek van het stoftransport bij Vallisneriabladeren gewezen, waardoor inzicht verkregen is in de stofwisselingsprocessen, die met opname en transport samenhangen. Bij dit object is het ook mogelijk geweest aan te tonen, dat in een bepaald geval het transport door de vaatbundel in tegenstelling met dat door de parenchymcellen door azid wordt geremd. Het is nodig zowel bij parenchymcellen als bij zeefvaten meer te weten over de stofwisselingsprocessen, die bij de opname en het transport betrokken zijn. Pas daarna zal men het mechanisme van opname en transport op bevredigende wijze kunnen verklaren.

COMMISSIE VOOR DE BIOSOCIOLOGIE

P. J. C. Kuiper: Verlandingsvegetaties in N. W. Overijsel

Bij de verlanding van open water kunnen we twee verschillende milieu's onderscheiden.

1. een eutroof milieu op plaatsen, waar de zandbodem dieper dan 2.50 m. beneden de waterspiegel ligt, of waar de zandbodem met een laagje zeeklei is bedekt, of op plaatsen waar leemlagen in de zandgrond voorkomen. Dit eutrofe milieu treffen we vooral aan in het Westelijk deel van het moerasgebied, in een brede strook langs de vroegere Zuiderzee.
2. een kwelmilieu op plaatsen waar uit de zandbodem grondwater omhoog kwelt en dat zich kenmerkt door een bruin neerslag van ijzerfosfaat aan de waterspiegel. Het verschijnsel van de kwel treedt op in een brede strook moeras gelegen tegen het Drentse plateau of het Hoge Land van Vollenhove.

De verlandingsvegetaties in het fosforarme kwelmilieu behoren tot het verbond *Caricion lasiocarpae* v. d. Bergen. (verbondskensoorten *Carex diandra, C. lasiocarpa, C. rostrata, Menyanthes trifoliata, Comarum palustre, Eriophorum gracile, Utricularia intermedia* en met een karakteristieke mossencombinatie van *Scorpidium scorpidioides, Campylium stellatum, Riccardia sinuata, Marchantia polymorpha var. aquatica, Fissidens adianthoides* e. a.). We kunnen een initiale fase onderscheiden, waarin nog waterplanten optreden en open water voorkomt, vervolgens treedt in de successie een *Scorpidium*-fase op (zie de bovengenoemde mossoorten), waarna door isolering t. o. v. het grondwater *Sphagnum*-groei optreedt, welke *Spagnum* -fase in hoogveen overgaat *Spagnion fusci*), tenzij door struikopslag bos ontstaat.
Door de vervening ontstonden lange petgaten, die afhankelijk van hun breedte en diepte drie verschillende reeksen van verlandingen te zien geven.

In zeer rustig milieu (breedte van het petgat minder dan 20 m.

bij een diepte groter dan 2 m., tot 40 m. breed bij een diepte van 1 m.) treedt de verlandingsreeks van het floristisch zeer rijke *Caricetum diandrae* op (kensoorten *Carex buxbaumii, Calamagrostis neglecta,* diff. soorten t.o.v. de ander 2 verlandingsreeksen o.a. *Parnassia palustris, Sagina nodosa, Linum catarcticum,* hoge abundantie van *Liparis loeselii, Dactylorchis sp., Eriophorum gracile,* aspect bepaald door *Carex diandra*). In de vegetatie van *Stratiotes aloides* treedt een begroeiing van *Equisetum fluviatile* en *Calamagrostis neglecta* op (*Calamagrostetum neglectae,* Steffen), die overgaat in de *Scorpidium* -fase van het *Caricetum diandrae.* Na maaien ontstaat een *Cirsieto-Molinietum,* bij niet maaien de *Spagnion*-fase en later een vegetatie van het *Spagnion fusci.* In minder luw milieu of in gedeeltelijk verveend terrein treedt de verlandingsreeks van het *Menyantheto-Juncetum subnodulosi* op, waarvan het aspect bepaald wordt door *Menyanthes trifoliata* en *Juncus subnodulosus.*

In breed uitgeveende petgaten treedt de verlandingsreeks van het *Caricetum lasiocarpae* op, waarvan het aspect wordt bepaald door soorten als *Phragmitis communis, Typha angustifolia* en *Carex lasiocarpa.* Ook bij deze reeksen gaat de verlanding van een initiale fase naar een *Scorpidium*-fase, een *Spagnum* -fase en een *Spagnion* fusci.

In eutroof milieu treffen we in hoofdzaak twee verlandingsreeksen aan, een in luw en een in winderig milieu.

In luw milieu treedt het *Hydrochareto-Stratiotetum* op, die overgaat in het *Cicuteto-Caricetum pseudocyperus,* de drijftillengemeenschap. Deze gaat op zijn beurt over in vegetaties van *Carex paniculata, C. acuta, C. acutiformis* e.a., welke successie meestal eindigt in het *Thelypterideto-Alnetum,* het elzenbroek.

In winderig milieu zien we het *Myrriophylleto-Nupharetum,* dat verland door soorten als *Scirpus lacustris, Typha angustifolia, Cladium mariscus* en *Phragmitis communis,* waarvan het voorkomen wordt bepaald door prioriteit en kleine milieuverschillen t.a.v. de golfslag. Dit gaat over in het *Thelypterideto-Phragmitetum,* fase van *Acrocladium cuspidatum,* welke overgaat in een *Spagnum*-fase en vervolgens in een vegetatie van het *Spagnion fusci.* In het *Thelypterideto-Phragmitetum* komen door isolerende werking van het veen mesotrofe plekken voor, die floristisch herinneren aan het kwelmilieu: *Liparis loeselii, Comarum palustre, Carex diandra.* De overige kenmerkende soorten uit het kwelmilieu ontbreken echter, terwijl het aspect bepaald wordt door *Dryopteris thelypteris,* een typische indicator voor eutroof milieu.

Dr. D.M. de Vries: Indicatie door graslandplanten

Er zit wat waars in de mening van Clements (1928), dat elke plant een indicator is. Elke soort wijst wel ergens op, zij het echter in meer of mindere mate. De indicatie kan op één standplaatsfactor betrekking hebben of op meer. De soorten, die een complex factoren aanduiden, zijn uiteraard voor de vegetatiekunde van het grootste belang. Verreweg de meeste plantensoorten wijzen pas iets aan, indien zij veelvuldig voorkomen, vandaar, dat door spreker in 1950 onderscheid is gemaakt tussen presentie- en frequentie-indicatoren.

Aannemelijk wordt gemaakt, dat combinaties van soorten grotere indicatorische waarde hebben dan de soorten afzonderlijk. Dit geldt in het bijzonder voor combinaties van soorten met hoge frequentie. Een overzicht wordt gegeven van het milieu der belangrijkste soortencombinaties van het grasland, die op objectieve wijze werden bepaald door berekening van de correlaties van voorkomen der soorten.

Met nadruk wordt er op gewezen, dat het gebruik van planten als indicator oordeelkundig moet geschieden. Als regel zal men op zoveel mogelijk soorten dienen af te gaan en men zal verdacht moeten zijn op schijnverbanden, veroorzaakt, doordat sommige milieu-factoren sterke koppeling vertonen. Ook is het mogelijk, dat de indicatie onder verschillende omstandigheden anders is, b.v. wat de kali betreft, bij verschillende gebruikswijzen van het land. Sommige hooilandsoorten blijken namelijk in hooilanden minnend, indifferent of zwak mijdend te zijn ten opzichte van K, terwijl dezelfde soorten in weilanden sterk mijdend zijn tengevolge van de verdringing door de echte, sterk K-minnende weidegrassen.

Tot slot wordt de verklaring van de begrippen „minnend" en „mijdend" onder het oog gezien. Dit zijn plantengeografisch gegroeide termen, die de mate van voorkomen voor de betreffende milieu-factor aangeven. Uit het feit, dat de potentiele amplitude (in reincultuur) vaak veel ruimer is dan de actuele amplitude, blijkt wel het grote belang van de concurrentie hierbij. De concurrentiekracht wordt echter behalve door het erfelijk vastgelegde concurrentie-vermogen door het milieu bepaald. De werkelijke oorzaak van het verschillend gedrag ten opzichte van plantenvoedende stoffen wordt aldus gedacht, dat mijdende soorten de betreffende stof gemakkelijk opnemen, minnende daarentegen moeilijk. Spreker is tot deze werkhypothese gekomen door combinatie van gegevens van het eigen correlatief oecologisch onderzoek te velde en van proefvelden, met de resultaten van potcultures van Dr. W. Dijkshoorn. Onafhankelijk hiervan kreeg Dr. M.A.J. Goedewaagen en Ir. J. Prummel ongeveer terzelfder tijd hetzelfde inzicht bij de beschouwing van de resultaten van een fosfaatvakkenproef.

W. Donselaar-Ten Bokkel Huinink: Successie-onderzoek van moeras-vegetaties door analyse van plantenresten in de bodem.

De beste methode voor successieonderzoek is de jarenlange controle van permanente quadraten. Wanneer in korte tijd een indruk van een bepaalde successiereeks verkregen moet worden, zijn andere methoden noodzakelijk. Bij verlandende plassen is het mogelijk, dat de zonering een afspiegeling van de successie geeft, zekerheid daarover is echter vaak moeilijk te krijgen.

De successie in drie dode rivierarmen werd bestudeerd met behulp van een nieuw ontworpen methode. De theoretische achtergrond hiervan is als volgt aan te duiden: dode plantenresten bezinken in water, uit de vertikale rangschikking van deze resten op de bodem moet de successie te reconstrueren zijn, mits aan de volgende voorwaarden is voldaan:

1e. de plantenresten moeten zo goed geconserveerd zijn, dat ze door vergelijking met vers materiaal te determineren zijn.
2e. de snelheden, waarmee de resten van de verschillende soorten vergaan mogen niet te zeer verschillen.
3e. de resten moeten bezinken op de plaats waar ze gevormd zijn.

De eerste voorwaarde bleek in alle drie de gebieden vervuld, de tweede werd nagenoeg in orde bevonden door vergelijking van de soorten en hoeveelheden en resten op verschillende plaatsen en diepten. Wat de derde voorwaarde betreft waren er verschillen, die met de waterhuishouding van de oude lopen bleken samen te hangen. In een kleine binnendijkse oude loop met stilstaand water werd, uiteraard autochtoon, een kleiïg veen afgezet. De toestand bij twee buitendijkse oude lopen werd onderzocht door na een overstroming de bovenste plantenresten te vergelijken met de tegenwoordige vegetatie. Bij één van de twee, gelegen in een diepe bocht van de dijk, was de stroomsterkte tijdens de overstroming zeer gering en werden de plantenresten tezamen met veel klei ter plaatse gedetermineerd. In de andere, bij hoog water veel meer in de stroom opgenomen, werden de plantenresten kennelijk verplaatst. In de eerste twee gevallen werden met de methode betrouwbare resultaten verkregen. De conclusie is, dat de beschreven methode bruikbaar is mits aan de genoemde voorwaarden is voldaan. De onderzoeker moet echter de tegenwoordige vegetatie eerst bestudeerd hebben om de verkregen gegevens te kunnen interpreteren.

B. Zwart Jr.: Het veen op grote diepte onder Amsterdam

Nauwkeurige analyse van een 37 cm lange veenkolom, voorkomend op een diepte van 11,50-11,87 m. beneden N.A.P. (het veen werd om de 3 cm geanalyseerd) leerde ons, dat dit veen, gestoken in de Sloterpolder aan de westgrens van de nieuwe stadsuitbreiding, geheel in het Atlanticum was gevormd. Deze waarneming is in overeenstemming met een analyse van het veen op grote diepte onder de Westhaven van Amsterdam (uitgevoerd door de Rijksgeologische dienst), doch in tegenstelling met de datering van dit veen uit de tunnelput van Velzen, waar Dr. Florschütz de grens Boreaal-Atlanticum middenin de „veen"kolom plaatste.

Het veen op grote diepte onder de Sloterpolder bleek geheel opgebouwd als een mengsel van elzenbroekveen en varenveen (*Dryopteris thelipteris*), waarbij onderin de elzen, maar bovenin afwisselend varens en elzen de overhand hadden. Echte waterplanten ontbraken. De armoede aan soorten in het geanalyseerde pollen was opvallend: *Alnus* maakte op één diepte 98,5% van het boompollen uit, van de kruiden waren de varens overheersend (soms tot ruim 500%).

Ir. W G. Beeftink: De halophiele vegetatie en molluskenfauna van Skallingen.

Skallingen (Denemarken) is een uit duinen en schorren bestaande landtong, die de noordelijke afsluiting van het Waddengebied vormt. Uit publicaties van Iversen blijkt, dat sedert 1930 door sedimentatie op het z.g. Buitenschor het percentage afslibbare delen van de bodem is toegenomen. De bodem van het Binnenschor, dat dichter bij de duinen ligt en moeilijker door de zee kan worden bereikt, is waarschijnlijk bijna niet veranderd. De grond van het Buitenschor bestaat uit klei tot zavel, die van het Binnenschor uit zavel tot zand. Verdere milieugegevens: zoutgehalte vloedwater ± 30‰ NaCl, gemiddeld getijverschil ± 1.30 m., beweiding ontbreekt ter plaatse van het onderzoek.

Op de slikken en schorren van het Buitenschor komen de volgende associaties voor: *Zosteretum nanae*, *Salicornietum europaeae*, *Puccinellietum maritimae*, *Halimionetum portulacoidis*, *Artemisietum maritimae* en een enkel individu van het *Atripliceto-Agropyretum litoralis* (nom. nov). Op het Binnenschor komen voor: *Salicornietum europaeae*, *Puccinellietum maritimae*, *Armerieto-Festucetum* en *Saginetum maritimae*. Hierbij valt op, dat *Aster tripolium*, die in Nederland minstens een kensoort van de *Puccinellio-Salicornietalia* is, zich bijna geheel tot het *Puccinellietum maritimae* teruggetrokken heeft. *Spergularia marginata* (een kensoort van het *Puccinellio-Salicornion* in Nederland) bevindt zich hier alleen in het *Puccinellietum maritimae*.

De reactie van de vegetatie tengevolge van een milieuverandering c.q. de toename van het % afslibbaar manifesteert zich door: 1. Uitbreiding of achteruitgang van de soorten als rechtstreeks gevolg van de milieuverandering en 2. verschuiving van het evenwicht in de onderlinge beïnvloeding der organismen. Door de veldmethoden van de vegetatiekunde kunnen deze twee aspecten van de reactie der vegetatie niet gemakkelijk worden ontleed. Op het Buitenschor zien we een toename van *Halimione portulacoides* en *Limonium vulgare*. De volgende soorten zijn in amplitude en bedekking afgenomen of geheel verdwenen: *Puccinellia maritima*, *Suaeda maritima*, *Aster tripolium*, *Halimione pedunculata*, *Plantago maritima*, *Spergularia marginata*, *Glaux maritima*, *Juncus gerardi* en *Armeria maritima*. De eerste drie waarschijnlijk primair door de uitbreiding van *Halimione portulacoides* en *Limonium vulgare*, de andere vermoedelijk in eerste instantie door de milieuverandering. De uitbreiding van *Halimione portulacoides* en *Limonium vulgare* op het Binnenschor kan het gevolg zijn van een vergrote diasporenaanvoer vanaf het Buitenschor.

Vergelijking van de floristische samenstelling van het *Sagine-*

tum maritimae op de Kaloot, Terschelling en Skallingen maakt het waarschijnlijk, dat het slibgehalte in de bodem van deze associatie het hoogst is op de Kaloot en het laagst op Terschelling.

Op het buitenschor zijn van de Mollusken gevonden *Littorina litorea* (presentie-optimum in het *Salicornietum maritimae* of lager), *Littorina saxitalis* (presentie-optimum in het *Puccinellietum maritimae*) en *Hydrobia ulvae* (presentie 100% in het *Puccinellietum maritimae*). *Phytia myosotis* bereikt de noordgrens van het verspreidingsareaal in Sleeswijk-Holstein.

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COMMISSIE VOOR DE PLANTENSYSTEMATIEK

H. J. Venema: Het Nederlandse kwekerssortiment van het geslacht *Helenium*.

Het geslacht *Helenium* (*Compositae*), thuishorend in Noord en Centraal Amerika, telt 25 à 30 soorten. Daarvan zijn enkele soorten voor het merendeel aangeboden onder de namen *H. autumnale*, *H. bigelowii*, *H. bolanderi*, *H. hoopesii* en *H. nudiflorum*, in cultuur. In ons land worden thans ± 30 tuinvariëteiten van Helenium gekweekt. Wat door de Nederlandse kwekers onder deze namen wordt aangeboden, klopt echter niet altijd met de Amerikaanse beschrijvingen. Dat geldt b.v. voor *H. bolanderi*. Van *H. bigelowii* worden 2 variëteiten aangeboden: *var. aurantiacum* en *var. superbum*. Beide behoren echter niet tot *H. bigelowii* Gray. In hoeverre de tuinvariëteiten behoren tot de soorten *H. autumnale* en *H. nudiflorum* dan wel bastaarden zijn van deze 2 soorten, dat is niet zo gemakkelijk uit te maken. Van tuinbouwkundig standpunt is dat ook niet zo belangrijk.

Binnen het kader van de sortimentsonderzoekingen welke in samenwerking met de kwekers en met steun van de Landbouworganisatie T.N.O. doorgevoerd worden door het Lab. voor Plantensystematiek en -geografie te Wageningen, valt ook het controleren van de benamingen der cultuurvariëteiten. Daar type materiaal vrijwel steeds ontbreekt, de beschrijvingen veelal onvolledig zijn, soms zelfs met elkaar in strijd en de tekeningen veelal meer artistiek dan natuurwetenschappelijk verantwoord zijn, is de controle van de benamingen vaak zeer moeilijk, zo niet onmogelijk. In de tuinbouwliteratuur zijn de beschrijvingen der variëteiten vnl. gebaseerd op de kleur van de lintbloemen en het hoofdje, het bloeiseizoen en de hoogte der planten. Het blijkt echter dat er wel degelijk morfologische verschillen bestaan tussen de verschillende klonen, waaraan men bij de beschrijving onvoldoende of veelal zelfs in het geheel geen aandacht geschonken heeft. Dat zijn b. v. de vorm van de bloembodem, de variabiliteit van het aantal lintbloemen per hoofdje, kleur en vorm van de lintbloemen en van het vruchtbeginsel met de kelkslippen. Voorts de mate waarin de bladeren langs de stengel aflopen en het min of meer getand zijn van de bladeren. Eén en ander toont spreker aan met aquarellen van bloeiwijzen van in verschillende ontwikkelingsstadia zich bevindende bloemhoofdjes en tekeningen van de vorm en afmetingen der lintbloemen, vorm en afmeting van het vruchtbeginsel, de kelkslippen enz.

L. Bos: Teratologische verschijnselen bij *Tropaeolum*

In september 1955 werden in het Arboretum te Wageningen een aantal planten van *Tropaeolum majus L.* gevonden met gedrongen stengeluiteinden welke bezet waren met een groot aantal kleine bladeren. Ze wekten de indruk van heksenbezems. Deze „bezems" bleken grotendeels te bestaan uit bloemen, welke een grote variatie van interessante morfologische afwijkingen (teratologische verschijnselen) vertoonden.

Volgens de teratologische literatuur zijn bloemabnormaliteiten bij deze plantensoort reeds lang bekend (Penzig, 1921). Hier wordt echter nergens gesproken van heksenbezemvorming.

Bij nader onderzoek van de verschijnselen blijken hoofdzakelijk de bloemen afwijkingen te vertonen.

Naarmate de bloemen jonger zijn, d. w. z. later zijn aangelegd, dichter bij het uiteinde der stengels geplaatst zijn, zijn ze meer abnormaal en moeilijker als bloem te herkennen. De meest opvallende afwijkingen zijn: vergroening, fyllodie en prolificatie. De bloemafwijkingen blijken tenslotte niet te bestaan uit een chaos van abnormaliteiten, maar nauw samen te hangen. Ze vormen alle een zeer bepaald onderdeel van een samenhangende groep van antholyse (= bloemoplossing)-verschijnselen.

In volgorde aangelegde bloemen vormen aan de afwijkende planten op deze wijze een fraaie antholyse-reeks. In het materiaal van *Tropaeolum* zijn overgangsstadia van een normale bloem tot een vegetatieve tak met bladeren, bijzonder goed waar te nemen. Aan de hand van een serie lichtbeelden werden de meest karakteristieke stadia gedemonstreerd. Speciale aandacht werd geschonken aan de fyllodie van meeldraden, vruchtbladen en zaadbeginsels.

Bij antholyse groeit tenslotte zelfs de bloembladen door tot een zich sterk vertakkende dicht met bladeren bezette, vegetatieve spruit. Uiteindelijk vinden we op de plaats van bloemen, takjes welke naar vorm en rangschikking van de bladeren niet meer doen denken aan een bloem. Aan deze takjes lopen op grote schaal okselknoppen uit, terwijl aan de aldus ontstane zijassen hetzelfde zich herhaalt. Op deze wijze kunnen de stengeluiteinden van aanvankelijk normale planten zich ontwikkelen tot enorme en dichte heksenbezems.

Zo blijken bloemoplossing en heksenbezemvorming duidelijk samen te hangen; het eerste geeft tenslotte zelfs aanleiding tot het tweede. Daarom kan hier gesproken worden van een complex van heksenbezemverschijnselen.

Volgens de plantenziektekundige literatuur komen in Australië (Hill, 1943) en in Amerika (Severin & Freitag, 1945) o.a. bij *Tropaeolum* ziekteverschijnselen voor, veroorzaakt door een tweetal virussen, waarvan door ons vermoed wordt dat ze overeenkomen met de in Wageningen waargenomen en hier beschreven afwijkingen. Vermoed wordt dat ook hier sprake is van een virusziekte. Proeven om dit aan te tonen zijn nog gaande.

Zo hebben de heksenbezemverschijnselen behalve een morfologische betekenis (b.v. met betrekking tot de morfologische waarde van de bloem), als ziekteverschijnselen belangrijke betekenis voor de fytopathologie: hier is sprake van pathologisch-morfologische verschijnselen.

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B.K. Boom: Merkenrecht en Nomenclatuur

Hoe verschillend de interpretatie van sommige artikelen van de Code ook moge zijn, er is één punt, waarover allen het eens zijn nl. de vrijheid, die we hebben over een naam te kunnen beschikken. Niemand kan een ander beletten een bepaalde naam voor een taxon te gebruiken. In land- en tuinbouw is het evenwel met deze vrijheid reeds enige tijd gedaan speciaal sedert men de mogelijkheid heeft planten te laten patenteren en namen als merk te laten deponeren. Bij cultuurgewassen doen commerciële belangen hun intrede in de nomenclatuur en dit is een der redenen, waarom de benaming dezer planten geregeld wordt volgens een afzonderlijke Code. Doch ook in deze Code is in de mogelijkheid namen te beschermen niet voorzien.

Nu zijn de begrippen „merk” en „naam” volledig aan elkaar tegengesteld. Namen behoren tot het publiek domein en hebben steeds één bepaalde inhoud; namen kunnen niet gemonopoliseerd worden, een principe, dat aanvaard is in alle merkenwetten ter wereld. Merken (en hier zijn steeds woordmerken bedoeld) zijn eigendom van personen of firma's, die het uitsluitend recht hebben dit merk te gebruiken en ook het recht hebben het gebruik ervan aan een ander te verbieden; merken hebben geen bepaalde inhoud; indien iemand de inhoud ervan wenst te wijzigen, kan dit straffeloos geschieden. Merken voldoen dus niet aan de meest elementaire regels van de nomenclatuur en we kunnen ze dus ten hoogste rangschikken onder de nomina nuda.

Het gevolg hiervan is, dat bij de voorgenomen registratie namen van cultuurvariëteiten, de merken eigenlijk niet kunnen worden vermeld. Anderzijds is het noodzakelijk ze op te nemen, omdat de merken in de praktijk naamkarakter hebben en een lijst zonder deze merken verre van compleet zou zijn en daardoor alle waarde zou verliezen.

Er zal daarom naar een compromis moeten worden gezocht hetgeen wellicht hierin kan worden gevonden, dat bij de registratie van nieuwe namen de eigenaar verklaart in de toekomst de inhoud ervan niet te wijzigen. Aan de voorwaarde, dat een merk ook door het publiek gebruikt mag worden zal evenwel nooit kunnen worden voldaan, omdat daarmede de eigenaar van het merk in feite van zijn merkenrecht afziet en het woord ophoudt een merk te zijn.

De toekomst zal moeten leren, in hoeverre deze kwestie een effectieve benaming en registratie van variëteiten van cultuurgewassen in de weg zal staan.

R. van der Wijk: Distich en pseudodistich

Als kenmerk der *Phyllogoniaceae* wordt opgegeven dat de bladen distich zijn. Dat komt uit bij *Phyllogonium*, waar de bladen afwisselend in twee rijen langs de stengel staan. Maar bij *Eucatagonium* is dit anders. De bladen staan zo op 't eerste gezicht wel in twee rijen, maar bij nader toekijken is het toch heel anders dan bij *Phyllogonium:* de onderlinge afstanden der linkse resp. der rechtse bladen zijn ongelijk. En kijkt men dan nauwkeuriger, dan blijkt duidelijk, dat ze aan de samengedrukte (afgeplatte) stengel ook niet in twee rijen staan, maar in meer rijen. In hoeveel? Het is bekend, dat de bladstanden bij de Bladmossen dezelfde eigenschappen hebben dan bij de hogere Planten: het aantal verticale rijen is een getal van de hoofdreeks of rij van Fibonacci, dus 2, 3, 5, 8, 13, enz. (elke term is de som der beide voorgaande). Door nu deze bladstanden te tekenen aan een cilinderoppervlak en aan te nemen dat bij samendrukking de bladen links van de mediaan links gaan uitstaan en de bladen rechts van de mediaan naar rechts, toonde spreker aan, dat op deze manier een regelmatige opeenvolging van afstandsverschillen tussen de bladen moest optreden. Voor 8 rijen werden de onderlinge afstanden in de schijnbare linker rij van bladen 1, 2, 3, 2, 1, 2, 3, enz. Hetzelfde gold voor de bladen van de andere kant. Deze verschillen in afstand bleken nu inderdaad bij *Eucatagonium* aanwezig. De conclusie was dus dat de bladen in 8 rijen stonden, octostich waren, maar door de samendrukking schijnbaar distich, vandaar de term pseudodistich.

Bij het derde geslacht *Orthorrhynchium* is de ene soort *O. elegans* distich en *O. cylindricum* pseudodistich. Hierin is dus een reden te vinden om ook de andere delen van deze beide soorten aan een nader onderzoek te onderwerpen. Nu blijkt het kapsel van *O. cylindricum* ongesteeld en opvallend lang cylindervormig en dat van *O. elegans* gesteeld en bijna-ovaal. Uit deze gegevens kan de conclusie getrokken worden dat *O. cylindricum* niet tot *Orthorrhynchium* behoort en waarschijnlijk niet eens tot de *Phyllogoniaceae*. Zo kunnen beschouwingen over de bladstanden ook bij de Bladmossen soms het systematisch inzicht verhelderen.

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Mej. G. R. van Hees (1948), Leiden, Rijnkade 3.
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W. H. A. Hekking (1955), Utrecht, Zuilenstraat 17.
Dr. R. J. Helder (1942), Groningen, Wassenberghstraat 54.
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W. M. Heyl (1920), Oegstgeest, Fred. Hendriklaan 33.
Mej. W. P. M. Hilbers (1952), De Bilt (Utr.), Emmalaan 12.
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